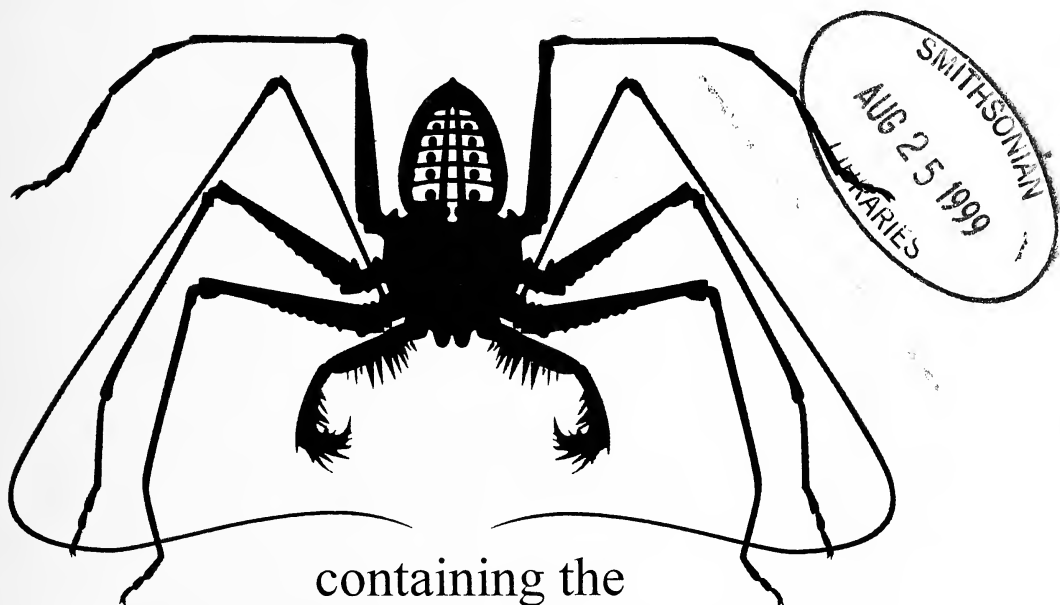


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The Journal of ARACHNOLOGY

OFFICIAL ORGAN OF THE AMERICAN ARACHNOLOGICAL SOCIETY



containing the
**Proceedings of the
XIV International Congress
of Arachnology**

and a
**Symposium on
Spiders in Agroecosystems**

THE JOURNAL OF ARACHNOLOGY

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ACKNOWLEDGMENTS

An historic event transpired between the 27th of June and the 3rd of July in 1998. I am indebted to more than three hundred arachnologists who gathered at the Field Museum of Natural History in Chicago, Illinois, USA to make the combined meeting of the International Congress of Arachnology and the American Arachnological Society a giant success. I think I speak for the entire American Arachnological Society when I say how delighted we were to be able to combine our 22nd meeting with the XIV International Congress and host the event in North America. This volume, in one sense the culmination of the meetings, stands as lasting documentation of the vast array of research publications that formed the core of these meetings.

The success of these meetings hinged on the hard work and dedication of a number of individuals who contributed in both large and small ways. Special thanks go to Petra Sierwald whose hard work and attention to detail ensured that we all had a good experience in Chicago. We also appreciate the cheerful support of the students and staff at the Field Museum throughout our visit. Thanks also go to Richard Bradley, Alan Cady, Karen Cangliosi, Jonathan Coddington, Fred Coyle, Matthew Greenstone, Gustavo Hormiga, Otto Kraus, Patricia Miller, Norman Platnick, Robert Raven, Gail Stratton, Robert Suter, Keith Sunderland, George Uetz, Betsy Berry, Rudiger Bieler, and Marius van der Merwe making significant contributions to the event. My apologies to those whom I have forgotten or whose contributions I failed to notice. Please know you have my gratitude as well.

The quality of the meetings were greatly enhanced by the two symposia. My sincere appreciation goes to Matthew Greenstone and Keith Sunderland for organizing a symposium on "Spiders in Agroecosystems" and to Gustavo Hormiga and Jonathan Coddington for organizing a symposium entitled "Higher Level Phylogenetics of Spiders." Thanks also to all the symposium participants.

It was fortunate that the American Arachnological Society was able to subsidize meeting costs, defray some of the travel expenses for participants, and support publication of this volume. The Centre International de Documentation Arachnologique also provided some support for this publication. The diligent efforts of Matthew Greenstone and Keith Sunderland secured extra funding to subsidize travel for the participants in their symposium and contribute to the publication of the proceedings.

The important and demanding task of assembling this volume cannot be overlooked. My heartfelt appreciation goes to James Berry, Brent Opell, and Matthew Greenstone who worked hard to bring us this high quality publication. Thanks also to all the reviewers who read and commented on all these manuscripts.

Finally, I am gratified by the high level and excellent quality of the student participation at these meetings. The excitement and commitment I saw in students from all over the world at these meetings reassured me that the future of arachnology is safe.

*Ann Rypstra, President
American Arachnological Society*

HISTORIC OVERVIEW OF PAST CONGRESSES OF ARACHNOLOGY AND OF THE CENTRE INTERNATIONAL DE DOCUMENTATION ARACHNOLOGIQUE (C.I.D.A.)

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ABSTRACT. In 1959, Hermann Wiehle encouraged junior colleagues to arrange a meeting for arachnologists. This was held in 1960 at the University of Bonn, Germany, and is counted as the first in the series of international congresses. After a second conference, held just one year later in Saarbrücken, Germany, a third truly international congress followed in 1965 in Frankfurt am Main. On this occasion, Max Vachon presented his idea to form what was later called the C.I.D.A. This institution was formally established at the occasion of the 4th congress, held in Paris in 1968. Detailed information on the origins, the series of congresses, and the C.I.D.A. up to 1968 is presented.

The state of arachnology during the first half of this century, and its condition following developments after World War II, differed strikingly. This is illustrated by two figures. Roewer's original catalog, and later supplementary entries, lists a total of 71 papers on spider systematics published in 1939. The equivalent figure for 1995 (according to the entries in Platnick's catalogue) is 268—almost four times more. This difference can only partially be explained by a world-wide increase in the number of universities and other research institutions, combined with an increasing number of researchers. Two other factors seem to be much more important: Air travel to foreign countries and world-wide personal contacts between researchers had become relatively easy. At the same time, primarily European conferences on arachnology quickly evolved into international congresses. The foundation of the "Centre International de Documentation Arachnologique"—the C.I.D.A.—in Paris, formed an integrative part of this development.

Traveling.—Up to the 1950s, most arachnologists did not know each other personally. They exchanged reprints, wrote kind (and other) letters; and they mainly traveled by train. Collecting and research work, especially in tropical countries, necessitated the organization of expeditions. Due to increasing international air travel facilities, this situation changed quite rapidly. American colleagues crossed the Atlantic, worked in European col-

lections and studied type materials; and personal contacts frequently resulted in firm friendships. As the western part of Europe recovered from the war, more and more European arachnologists were also able to go to other countries.

The aircraft most frequently used in those early days was the "Lockheed Super Constellation" with a cruising speed of 255 mph. Some people called it the world's safest three-propeller airplane, as there was a rumor that one of its four engines could occasionally be out of order. In these early days, Ernest Browning of the Department of Arachnology at the British Museum still prepared his endless lists for the Zoological Record by hand.

International organization and cooperation.—Most of those present in Chicago for the XIV International Arachnological Congress may not know how the flourishing series of International Arachnological Congresses originated, including the origins of C.I.D.A. So, I was asked, how it is that the present meeting is the 14th conference in the series. For these reasons, I will concentrate on the early history.

Late in 1959, the German arachnologist Hermann Wiehle (1884–1966, Fig. 1) conceived the idea that arachnologists should come together. Not only would this allow them to discuss scientific problems, but it would foster personal contacts and cooperation among arachnologists. Wiehle may be regarded as the initiator of our congresses. As



Figure 1.—Hermann Wiehle, the initiator of the International Congresses of Arachnology (photo taken on 23 April 1965 at the 3rd congress).

he lived in the eastern part of Germany (which was dominated by the Soviet Union at that time) and did not hold any office, he encouraged two junior arachnologists to arrange a meeting: Wolfgang Crome, curator at the Berlin Museum, and Ernst Kullmann, at that time scientific assistant at the University of Bonn.

As the next annual meeting of the German Zoological Society was scheduled to be held in Bonn, Kullmann used this meeting, in 1960, as a platform for hosting the arachnology conference. Approximately 20 German arachnologists attended (Fig. 2). The presence of Father Chrysanthus from the Netherlands, who worked on spiders from New Guinea, provided a bare minimum of international participation. Wiehle himself contributed a paper on "Der Embolus des männlichen Spinnentasters." Despite the fact that this study, based on functional morphology including aspects of co-adaptation between male and female genital structures, was of considerable importance and far ahead of its time, the topic remained almost completely neglected—even until now. Another contributor was Heinrich Homann who reported on retinal structures of spider eyes. Homann's landmark study con-

tributed greatly to our present understanding of certain aspects of aranaeomorph phylogeny.

Carl Friedrich Roewer, at this time nearly 80 years old, did not attend. Volume 2 of his "Katalog der Araneae," comprising 1751 pages, had been published in two voluminous parts five years previously. The availability of Roewer's completed catalog was a tremendous stimulus to araneologists. In principle, the information was arranged so perfectly that Paolo Brignoli, as well as Norman Platnick, had no reason to make major changes when they published four supplementary volumes in 1983, 1989, 1993, and 1997.

Everybody felt that meetings of arachnologists should be continued. Those present in Bonn resolved with enthusiasm that the next (second) conference should take place one year later (1961) in Saarbrücken. This was relatively close to the German/French border. Again, the annual meeting of the German Zoological Society was used as a vehicle. Kullmann had just accepted a position in Afghanistan for a couple of years. So I was asked to organize the meeting. The intention was to broaden the scientific basis and further to encourage attendance by colleagues from other European countries. This approach was successful: a large group of French arachnologists attended, including Pierre Bonnet and Max Vachon; and Peter van Helsdingen from the Netherlands also joined the meeting.

A gap of four years followed; but this was not at all a period of inactivity. In April 1964, Max Vachon came to Frankfurt for a couple of days and visited me, then curator at the Senckenberg Museum (Fig. 3). We discussed details of the forthcoming meeting of arachnologists to be held one year later, in 1965, in Frankfurt and, more importantly, how international cooperation in the field of arachnology could be improved. This was the conception, but not yet the birth, of C.I.D.A. Vachon, who was the last representative of the great French tradition, proposed the formation of an international organization which later became known as the "Centre International de Documentation Arachnologique." The Frankfurt congress was held from 21–25 April 1965. Originally, it was called "III. Treffen europäischer Arachnologen", but the designation "III. Kongreß europäischer Arachnologen" was used in the printed congress report (Senckenbergiana Biol., 47(1):1966). Fifty-

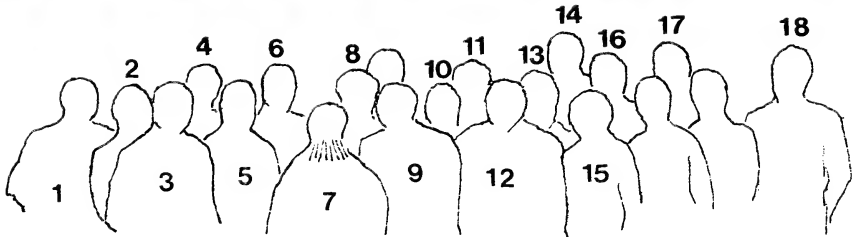


Figure 2.—Group of arachnologists at the first meeting in 1960 in Bonn. 1, G. Schmidt; 2, H. Casemir; 3, H. Homann; 4, B. von Broen; 5, H. Nemens; 6, R. Braun; 7, Father Chrysanthus; 8, H. Wiehle; 9, E. Kullmann; 10, Mrs. Kullmann; 11, H. Hiebsch; 12, R. Lehmensick; 13, M. Grasshoff; 14, W. Engelhardt; 15, Mrs. Crome; 16, W. Crome; 17, O. Kraus; 18, B. Heydemann.

three arachnologists were present. They came from Austria, Belgium, Czechoslovakia, Finland, France, Germany, Great Britain, Italy, Yugoslavia, The Netherlands, Poland, Ruma-



Figure 3.—Max Vachon vigorously discussing the foundation of the C.I.D.A. (conference held on 17 April 1964 at the Senckenberg-Museum, Frankfurt am Main).

nia and from Switzerland (Fig. 4). A business meeting was held, in which Vachon explained our joint ideas to establish the C.I.D.A. at the Muséum National d'Histoire Naturelle. He further proposed to meet three years later, in 1968, in Paris. These plans were unanimously accepted. Vachon started work as the "Secrétaire général permanent du C.I.D.A.," and I was elected as the first president of the organization just created. The C.I.D.A. was born! There are only a very few survivors who can still remember Wiehle's unforgettable "Rede über die Freundschaft" [lecture on friendship], held at the occasion of the farewell dinner. This perfectly reflected the general enthusiastic atmosphere.

Between 1965 and 1968, intensive contacts between Frankfurt and Paris followed. The world-wide system of C.I.D.A. correspondents was established, and details of the forthcoming meeting were carefully arranged. The Paris conference was officially called "IVème Congrès International d'Arachnologie." It took place from 8–13 April 1968, at the Mu-



Figure 4.—Pierre Bonnet (left) and G.H. Lockett (right) in conversation (photo taken on 23 April 1965 at the 3rd congress).

séum National d'Histoire Naturelle," a sacred place in arachnology. A total of 109 arachnologists from 23 nations attended, including participants from Algeria, Argentina, Canada, USA, India, Israel, Madagascar, Turkey, and Uruguay. The international scope was established step by step, but the fourth congress in Paris was the first which really had a worldwide scope. The program included no less than 60 contributions and the presentation of 11 scientific films (for details see the proceedings: *Bull. Mus. Natn. Hist. Nat.*, (2)41, Suppl. 1; 1969). Roger Legendre was elected as president for the forthcoming period. The congress participants accepted my proposal that the next meeting should be held in Brno, Czechoslovakia. The idea behind this was that more colleagues from eastern countries would obtain permission to attend. But this proved to be an error.

The fifth "Brno Congress" was held from 30 August–4 September 1971. Ninety-seven participants from 23 countries attended. Compared to the preceeding congress in Paris, there was only a slight decline in the number of arachnologists present, but only 6 colleagues came from countries outside Europe (Paris: 13). Officially, the congress was organized by the "Institute of Vertebrate Zoology," Director J. Kratochvíl. However, it was Dr. Vladimír Silhavy, a physician and qualified amateur arachnologist specialized in the Phalangida who did all the work. He also pre-

pared the congress proceedings. These were technically published in "1972" by the Institute already mentioned, but the publication was not issued until May 1973 as a separate volume.

From this point forward, a self-perpetuating cycle of international conferences was clearly established. Information on the succeeding congresses, numbered 6–13, is readily obtainable as their proceedings were published regularly and are accessible. So I simply mention places, countries and organizers: VI: Amsterdam (Netherlands), P. van Helsdingen.—VII: Exeter (UK), A.F. Millidge; VIII: Vienna (Austria), H. Nemenz and J. Gruber; IX: Panama City (Panama), M. Robinson; X: Jaca (Spain), M. Rambla; XI: Turku (Finland), P. Lehtinen; XII: Brisbane (Australia), R. Raven; XIII: Geneva (Switzerland), V. Mahnert.—It is noteworthy that only two out of these 13 congresses have been held outside Europe. This seems to be correlated with the geographical distribution of those arachnologists with access to substantial institutional assistance, financial resources and appropriate publishing facilities.

Concluding remarks.—Against this background, the present invitation by the American Arachnological Society to have this meeting, for the first time in the United States, is appreciated. We are extremely grateful to Petra Sierwald and her collaborators for undertaking the laborious task. But we should also express our sincere thanks to the people of the C.I.D.A. Secretariat in Paris, to Mme. Jacqueline Heurtault and her co-workers. This institution, established in 1964, has functioned perfectly since 1968. The annual information service provided by the C.I.D.A. was extraordinarily useful. It was this institution that helped safeguard the series of our international congresses, which has not been interrupted since 1965. Now, the celebration of C.D.I.A.'s 30th birthday coincides with the end of the original Paris secretariat—due to complications caused by organizational and personal problems. But fortunately, the headquarters will move from the Paris museum to the National Museum of Natural History in Washington, D.C., and the work will be continued by J. Coddington as Secretary General (Washington), Robert Raven as current president (Brisbane, Australia) and N. Platnick as membership secretary (New York).

THE GENUS *ATTIDOPS* (ARANEAE, SALTICIDAE)

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ABSTRACT. The genus *Attidops* is resurrected from *Ballus* based on its strongly excavate cymbial tip, transverse embolar groove, flatter carapace with extended postocular area, and single retromarginal cheliceral tooth, which indicate a closer relationship to the genus *Admestina*. The type species, *Ballus youngii* Peckham & Peckham 1888, again transferred, becomes *Attidops youngi* (Peckham & Peckham). Two new species, *Attidops nickersoni* (sister species to *A. youngi*) and *Attidops cutleri*, are described. *Icius cinctipes* Banks 1900, previously transferred to *Ballus*, becomes a new combination, *Attidops cinctipes* (Banks). Lectotypes and paralectotypes are designated for *Ballus youngii* and *Icius cinctipes*. The genus is recorded from south-central Canada, eastern U.S. and eastern Mexico.

Banks (1905) created the genus *Attidops* in a footnote, stating simply “*Attidops*, a new genus for *Ballus youngi* Peck.” The Peckhams (1909) refuted this genus, asserting that, “. . . *Youngii* is so close to the type of *Ballus* (*depressus*) that Mr. Emerton, in a letter to us, has suggested that it may be identical. We think that it [*youngi*] differs enough to be a good species, but it clearly belongs to the genus *Ballus*, and hence we treat *Attidops* as a synonym.” Unfortunately, none of these authors offered any morphological evidence supporting or refuting the placement of *B. youngi* in *Ballus*. Kaston (1948) later addressed this issue: “although *Ballus* is considered a pluridentate genus, all the specimens of *youngii* seen by me have only a single retromarginal tooth. There may be justification for removing *youngii* to the genus *Attidops* set up for it by Banks (1905).” Quotes are as originally published, except name in brackets is my insertion.

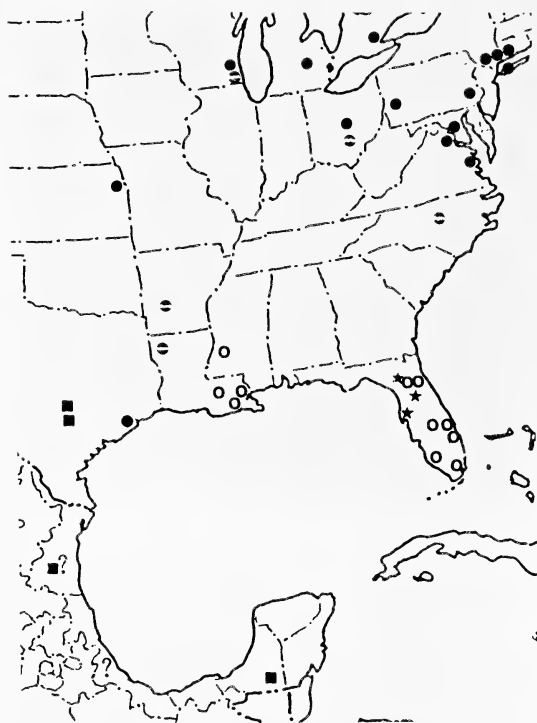
European species of *Ballus* C.L. Koch 1851 have been revised by Alicata & Cantarella (1987) with good illustrations of the genitalia, and Roberts (1985b: plate 59) illustrated in color the female dorsum of *Ballus chalybeius* (Walckenaer 1802) (as *Ballus depressus*). *Aranea depressa* Walckenaer 1802 (the type species of *Ballus*), which has page priority over *Aranea chalybeia* Walckenaer 1802, is pre-

occupied by *Aranea depressa* Razoumowsky 1789. *Admestina* Peckham & Peckham 1888, a genus consisting of three small, bark-dwelling species known from eastern North America, has also been revised (Piel 1991). In order to ascertain relationships, I compared specimens of the type species of all three putative genera: *Attidops youngi*, *Ballus chalybeius*, and *Admestina tibialis* Peckham & Peckham 1888. I concluded that *Attidops* is more closely related to *Admestina* than it is to *Ballus*, therefore I resurrect *Attidops*. *Icius cinctipes* Banks 1900, which I previously transferred to *Ballus* (Edwards 1980), also belongs in *Attidops*. In addition, two new species belonging to *Attidops* are described below.

METHODS

Measurements (in mm) of carapace length (CL), carapace width (CW), body length (BL), and legs were made with a calibrated ocular reticule in a Leica MS5 binocular microscope. If available, five specimens of each sex were measured; primary type measurements are given in parentheses within the range of variation of each species. A camera attachment was used to photograph dorsal views of specimens. Male and female genitalia were dissected, mounted in depression slides, and photographed through a Nikon Labophot compound microscope. All photographs were digitized, computer enhanced, printed, and retouched with black and white inks to produce most of the figures. Other abbreviations used are: anterior median eyes (AME), anterior lat-

¹Contribution No. 866, Bureau of Entomology, Nematology and Plant Pathology–Entomology Section.



Map 1.—Distribution of *Attidops* species: ● = *A. youngi* (divided circles = literature records), ★ = *A. nickersoni* new species; ■ = *A. cutleri* new species, ○? = *A. cinctipes*. Québec literature record of *A. youngi* not shown.

eral eyes (ALE), posterior median eyes (PME), posterior lateral eyes (PLE), anterior eye row (AER), posterior eye row (PER), and ocular quadrangle (OQ; the area bounded by the ALE and PLE). Eyes are included in the measurements of eye row width and OQ length. All illustrations of male palpi are of the left palpus.

I follow Platnick (1989) in considering Bonnet's corrections of patronyms ending in *-ii* as valid emendations of incorrect original spellings. Possible sites of obscure localities were found with <http://mapping.usgs.gov/> www/gnis/gnisform.html.

TAXONOMY

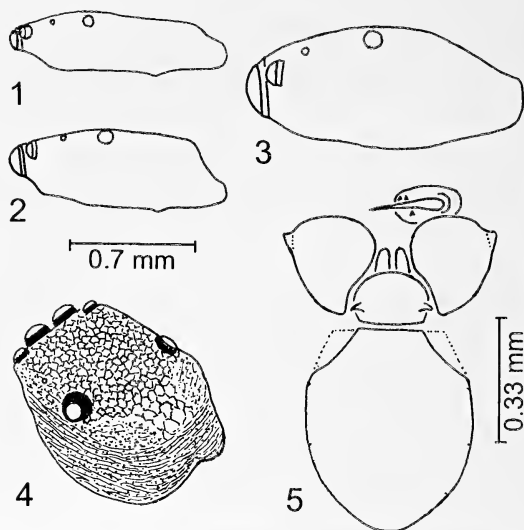
Attidops Banks 1905

Map 1

Attidops Banks 1905: 321 in footnote

Attidops: Peckham & Peckham 1909: 586 (= *Ballus*)

Type species.—*Ballus youngii* Peckham & Peckham by monotypy.



Figures 1-5.—Prosomal views. 1-3, lateral view of female carapace. 1. *Admetista tibialis*; 2. *Attidops youngi*; 3. *Ballus chalybeius*; 4-5, Male *Attidops youngi*. 4. Posterolaterodorsal view of carapace showing surface reticulations; 5. Venter of prosoma minus legs, free segments of palpi, and one chelicera. Figures 1-4 to same scale.

Diagnosis.—Carapace flat as in *Admetista* (Fig. 1), but postocular dorsum (from PLE to top of thoracic slope) extended about equal to length of OQ (Fig. 2). The cymbium is strongly excavate distally on the retrolateral side, and the embolar groove is transverse. The embolus is situated distally and makes 1.5-3 spirals. The lateral portion of the tegular duct has a well-developed median bend. The gonopores of the epigynum are medial in transverse slits or a transverse depression. The epigynal plate is triangular, as in *Admetista*, although in *Attidops* the anterior epigynal edge is not well-defined. Tibia I not enlarged nor abdomen elongated as in *Admetista*. In *Admetista*, the postocular dorsum extends at least $1.25\times$ length of OQ, the cymbium is only slightly excavate, the embolus is canted to the retrolateral side and is a single spiral, and the gonopores are anterior. In *Ballus*, the carapace is not as flat, the postocular dorsum extends only about $0.5\times$ length of OQ (Fig. 3), the cymbium is not excavate, the embolar groove is longitudinal, the embolus has more than 3 spirals mostly fused together, and the gonopores are in submedian longitudinal slits.

Description.—Small spiders, 2.1-3.1 in length, carapace length 1.0-1.3, width 0.8-1.1

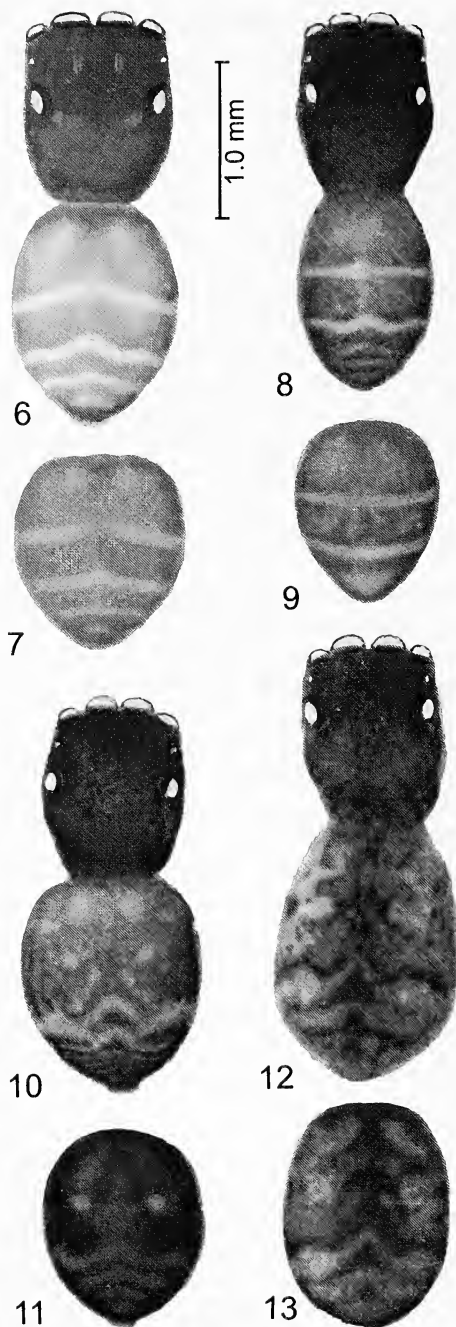
at widest point behind PLE and half as high as wide in middle, length of OQ plus AME almost half length of carapace; PME tiny, on line between dorsal edges of ALE and PLE, slightly closer to ALE (0.46 distance from ALE to PLE). Prosoma: carapace dark reddish-brown, darker around eyes; vertical laterally, flat dorsally with slight slant downward from PLE forward; postocular dorsum extends about the length of the OQ behind the PLE; thoracic slope is abruptly steep (but not vertical) and slightly concave; carapace integument (Fig. 4) entirely reticulate (reticulations polygonal on OQ, granular tending toward anastomosing striations laterally and posteriorly), polygonal reticulations extending posterior to PER medially to top of thoracic slope; chelicerae small, two adjacent promarginal teeth, one opposing retromarginal tooth; endites semitruncate distally with corners rounded, with a slight flange or incipient cusp in males on outer distal corners; labium slightly wider than anterior margin of sternum, with minute, transverse, sclerotized ridge each side posterolaterally (Fig. 5); venter and legs reddish- to yellowish-brown (pale yellow in *A. cinctipes*); legs IV, I, II, III in order of length, both sexes similar; legs I only slightly broader than legs II-IV, legs with brown maculations. All tarsi and metatarsi pale yellow with proximal brown annulae. Leg measurements given only for *A. youngi*, as all four species are similar, and legs are proportional to body size. The only macrosetae present (all ventral) are: leg I: metatarsus 2-2 (distal and median), tibia 2-1 or 1-0 (median and proximal); leg II:

metatarsus 1 (median), tibia 1 (median). Male palp with femur concave ventrally; sperm duct, upon traversing distal haematodocha, enters a membranous to sclerotized apparent embolus base which forms a core which is surrounded by a spiralled, flat, mostly membranous to mostly sclerotized embolus. Opisthosoma (abdomen): 0.8-1.4 wide; dorsum reddish brown with an anterior pair of submedian pale integumental spots, followed by two or three complete, narrow, pale transverse bands, followed by a few partial median transverse bands (all partially obscured in *A. cinctipes*); in males, dorsum completely covered with a translucent scutum (not obscuring pattern); venter pale to reddish-brown, without maculations (except *A. cinctipes*). Entire body with sparse covering of short white setae and translucent clear to white "scales" (flattened adpressed setae), especially laterally.

In addition to the above mentioned differences, *Ballus* has two or three teeth on a raised portion of the cheliceral retromargin ("serrated platelet"; Alicata & Cantarella 1987), the labium lacks modifications, anteriorly the carapace is inclined noticeably downward from the PME, the posterolateral areas of the carapace are concave, the thoracic slope is gradually inclined, the lateral portion of the tegular duct has the median bend barely noticeable, and the epigynum is rectangular with the anterior margin of the epigynum well-defined. In size, species of *Ballus* are mostly longer than (2.5-5.0: Roberts 1985a; Alicata & Cantarella 1987) and have more mass than (since they are not as flat) species of *Attidops*.

KEY TO THE SPECIES OF *ATTIDOPS*

- 1. Integument mostly pale (except carapace), with symmetrical dark maculations on legs and on abdomen (both dorsum and venter) (Figs. 12-13); embolus heavily sclerotized, 1.5 spirals (Figs. 24-25); gonopores in submedian transverse slits (Figs. 26-27); Gulf states of U.S. (and Mexico?) *cinctipes* (Banks)
- Integument mostly dark reddish brown, with narrow pale transverse bands on abdominal dorsum; abdominal venter immaculate; embolus with 2 or 3 spirals; gonopores in transverse depression 2
- 2. Embolus mostly sclerotized, 2 spirals (Figs. 22-23); gonopores in posterior depression (Figs. 29-30); abdominal transverse bands broken and/or fused (Figs. 10-11); Texas, Gulf states of Mexico *cutleri* Edwards
- Embolus mostly membranous, 3 spirals (Figs. 14-15, 18-19); gonopores in lobed median depression (Figs. 16-17, 19-20); abdominal transverse bands distinct 3
- 3. Three complete transverse abdominal bands, two pair small white spots on OQ (Figs. 6-7); south-central Canada, eastern U.S. except lower Southeast *youngi* (Peckham & Peckham)
- Two complete narrow transverse abdominal bands; no OQ spots (Figs. 8-9); central Florida ... *nickersoni* Edwards



Figures 6–13.—Female dorsum, male dorsal abdomen of species of *Attidops*. 6–7. *A. youngi*; 8–9. *A. nickersoni* new species; 10–11. *A. cutleri* new species; 12–13. *A. cinctipes*.

Attidops youngi (Peckham & Peckham 1888)
Figs. 2, 4–7, 14–17

Ballus youngii Peckham & Peckham 1888:87, Plate
1 Fig. 66 (♀ abdominal dorsum), Plate 6 Fig. 66,

66a (♂ palp), 66b (epigynum); Cotypes (♂ palp; 3♀, one missing epigynum) from USA: *Pennsylvania*: Allegheny County, under bark (usually hickory and sycamore), November (J.J. Young, MCZ), examined [data from description]; ♀ lectotype, 3 paralectotypes designated

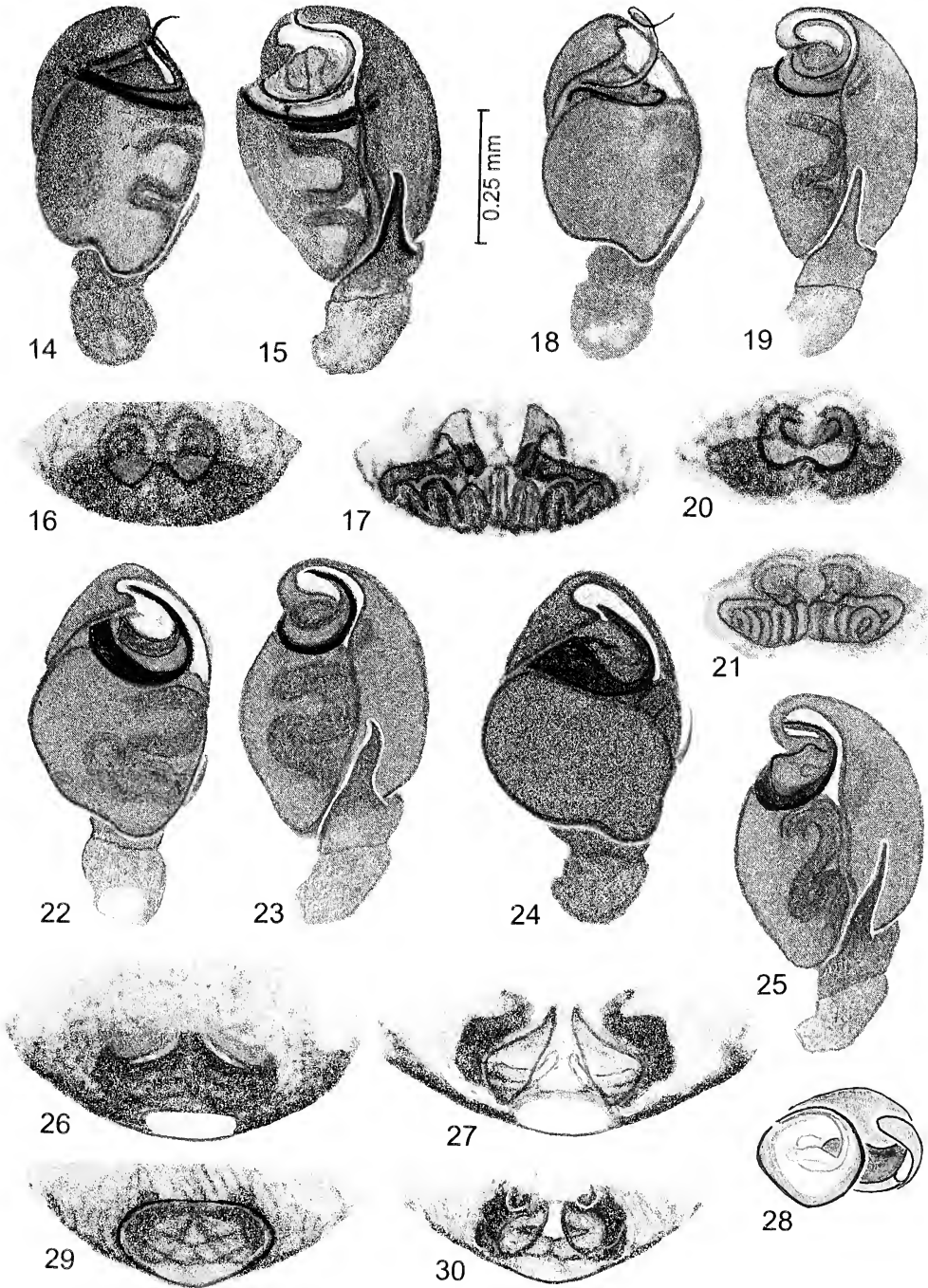
B. youngi: Marx 1890:576 (-ii); Banks 1895:92, 1899:190; Simon 1901:485; Peckham & Peckham 1909:586 (-ii), Plate 49: Figs. 9, 9a (♂ palp), Plate 51: Figs. 13, 13a (♀ abdomen, epigynum); Petrunkevitch 1911; Comstock 1913:671 (-ii); Crosby & Bishop 1928; Kaston 1938:195 (-ii), 1948:447 (-ii), Figs. 1621 (epigynum), 1622 (palp); Roewer 1954:973 (-ii); Bonnet 1955:848; Levi & Field 1954:462 (-ii); Dorris 1968:36 (-ii); Berry 1970:104; Richman & Cutler 1978:83; Stietenroth & Horner 1987:237; Bélanger & Hutchinson 1992:71 (-ii)

Attidops youngi: Banks 1905:321, 1910:74; Barrows 1918:315

Diagnosis.—Carapace with two pairs of white spots. Abdomen with three white, narrow, transverse abdominal bands, of which the second band is noticeably bent forward in the middle. Embolus mostly membranous and starts ventrally, with three spirals; embolus base membranous. Epigynum with a lobed, central, shallow pit containing the gonopores, which open near the center on the lateral edges of the lobe; ducts convoluted and diverted laterally.

Description.—Female CL 1.14 (1.15)–1.30, CW 0.89 (0.90)–1.00, BL 2.40 (2.65)–2.70; male CL 1.15–1.25, CW 0.87–0.98, BL 2.35–2.75. Embolus sclerotized on outer edge, sperm duct on inner edge. Carapace with two pair of small white spots (patches of scales), one pair about the middle of the OQ, the other pair posteromedial to the PLE; AER about 0.87 the width of the PER. Legs with femora, patellae, and tibiae brown laterally. Leg segment lengths of typical female (in order legs I–IV): femora (0.39, 0.32, 0.31, 0.42), patellae (0.23, 0.20, 0.16, 0.21), tibiae (0.19, 0.17, 0.17, 0.27), metatarsi (0.15, 0.15, 0.15, 0.24), tarsi (0.16, 0.16, 0.16, 0.17). First transverse abdominal band often broken in middle; rarely a nearly complete fourth transverse band present posteriorly.

Distribution.—South-central Canada and eastern United States from Connecticut to North Carolina, west to Wisconsin, and south to eastern Texas; under the bark of deciduous hardwoods (elm, shagbark hickory, sycamore) and hemlock. Literature records for which I



Figures 14–30.—*Attidops* genitalia. 14, 18, 22, 24. Palpi, ventral view; 15, 19, 23, 25. Palpi, retrolateral view; 28. Palpus, distal, slightly retrolateroventral view, cymbium removed; 16, 20, 26, 29. Epigyna, ventral view; 17, 21, 27, 30. Epigyna, dorsal view; 14–17. *A. youngi*; 18–21. *A. nickersoni* new species; 22–23, 29–30. *A. cutleri* new species; 24–28. *A. cinctipes*.

have not seen specimens are those of Banks (1899) from Louisiana, Barrows (1918) from Ohio (Rockbridge), Bélanger & Hutchinson (1992) from Québec, Berry (1970) from North Carolina, Dorris (1968) from Arkansas, and Levi & Field (1954) from Wisconsin.

Material examined.—**CANADA:** *Ontario:* Halton County, Burlington, Lamb's Hollow, 1 August 1985, 1 ♀ (W. Maddison, MCZ); **USA:** *Connecticut:* Fairfield County, Shelton, 7 April 1935, 1 ♀ (B.J. Kaston, USNM); New Haven County, Mt. Carmel, 15 April 1935, 1 ♂ 1 ♀ (B.J. Kaston, USNM); South Meriden, 31 March 1935, 2 ♂ (H.L. Johnson, USNM); *Kansas:* Jefferson County, Nelson Environmental Area, 24 January 1994, 1 juv (H. Guarisco, HGC); *Maryland:* Montgomery County, Silver Spring, 28 September 1944, 1 ♀ (M.H. Muma, FSCA); *Michigan:* Livingston County, E.S. George Reserve, June–August 1951–1957, 13 ♂ 19 ♀ 4 juv (all H.K. Wallace, FSCA); *New York:* Nassau County, Sea Cliff, 1 ♂ 1 ♀ 2 juv (2 vials) (N. Banks, MCZ); Orange County, Harriman, Bear Mountain State Park, 25 April 1964, 1 ♂ (J. & W. Ivie, AMNH); Westchester County, Yonkers, 14 January 1935, 1 ♀ 6 juv (R. Woodbury, USNM); *Ohio:* Knox County, Brinkhaven, on sandstone cliffs, 15 September 1917, 4 ♂ 3 ♀ (W.M. Barrows, OSU); *Pennsylvania:* Bucks County, northeast of Jamison, Horseshoe Bend, January–June and October 1954–1958, 63 ♂ 77 ♀ 14 juv (all W. Ivie, AMNH); *Texas:* Brazoria County, Otey, February 1971, 1 ♂ (K. Stephan, FSCA); *Virginia:* Arlington County, Cherrydale, 20 April 1935, 1 ♂ 1 ♀; 30 April 1935, 1 ♂ 3 ♀ (all R. Woodbury, USNM); York County, Site 5, 5 January 1984, 1 juv (C. Stietenroth, MSU); *Wisconsin:* [? Waukesha County, Pine Lake], 1 ♂ (Peckham, MCZ); [? *Alabama:* Lawrence County or *Texas:* Anderson County]: Green's Bluff, phoebe's nest, 5 November 1949, 1 ♂ 2 ♀ (FSCA). Brackets indicate possible resolutions of missing data.

***Attidops nickersoni* new species**

Figs. 8–9, 18–21

Types.—Holotype ♂, alloparatype ♀ together in one vial; 1 ♂ 6 ♀ paratypes in second vial, from **USA:** *Florida:* Marion County, Ocala National Forest, 1.8 miles west of FR 579 on FR 595 [older maps indicate as FR 79 and FR 95, respectively], under bark of living and dead longleaf pines, 13 November 1975 (G.B. Edwards and J.C.E. Nickerson, FSCA); 1 ♂ paratype, same locality, 6 November 1998 (P.E. Skelley, FSCA); 1 ♂ 3 ♀ paratypes, 2 miles west of FR 579 on FR 595, 29 September 1976 (G.B. Edwards, FSCA) [collected as penultimates, all matured October 1976].

Etymology.—Named after the late Dr. Everett Nickerson, fellow student of Dr. Willard H. Whitcomb, co-collector of the type series.

Diagnosis.—Proportionately narrower than *A. youngi*, and there are only two pale yellow, very narrow, transverse abdominal bands (the second sometimes has a slight median forward bend), followed (in preserved specimens) by a pale posterior triangular spot (which in females has 3–5 partial, median transverse bands). Embolus like *A. youngi*, but it starts retrolaterally. Epigynum like *A. youngi*, but proportionately smaller.

Description.—Female CL 1.13–1.20, CW 0.81–0.86, BL 2.17–2.40; male CL 1.10 (1.10)–1.15, CW 0.80 (0.80)–0.82, BL 2.25 (2.25)–2.30. Males with prolaterodorsal yellow stripe on all patellae and tibiae; otherwise legs marked as in *A. youngi*, but paler ventrally. The Gainesville specimen differs by having the most anterior band broken in the middle, and by having a third transverse band, also broken in the middle.

Distribution.—Central Florida, most records from under the bark of longleaf pine.

Material examined.—**USA:** *Florida:* Alachua County, Gainesville, under live oak bark, 30 November 1975, 1 ♀ (D.B. Richman, FSCA); Pinellas County, Dunedin, 1927, 1 ♀ (W.S. Blatchley, MCZ).

***Attidops cutleri* new species**

Figs. 10–11, 22–23, 29–30

Types.—Holotype ♂ from **USA:** *Texas:* Travis County, Austin, 18 October 1967 (D. Simon, FSCA); paratype ♂ from *Texas:* Caldwell County, Lockhart State Park, W97.40: N29.50, 13 April 1963 (W.J. Gertsch & W. Ivie, AMNH).

Etymology.—Named for Dr. Bruce Cutler, who first identified the AMNH specimens to genus.

Diagnosis.—Shorter than *A. youngi*, and the first transverse band broken into two spots (making two pair of spots anteriorly), the second transverse band (apparent first band) bent forward not only in the middle but once on each side as well, and all following bands bent forward in the middle. Embolus more sclerotized than membranous with two complete spirals, embolus base sclerotized. Epigynum with gonopores located in anterior part of large posterior depression; ducts less complex than *A. youngi*.

Description.—Female CL 1.0–1.0, CW

0.80–0.85, BL 2.2–2.2; male CL (1.05)–1.05, CW (0.86)–0.92, BL (2.15)–2.15. Legs marked as in *A. youngi*. Dorsum of abdomen with scattered symmetrical lateral pale markings; second and third transverse bands (usually the only two complete bands present) may be fused together laterally and somewhat broken medially in females. Overall color pattern gives the impression of being intermediate between *A. youngi* and *A. cinctipes*. Males and females have not been collected together, but the size, shape and color pattern of the specimens leads me to match them. The Tamaulipas female has underdeveloped insemination ducts and may be immature, therefore I have illustrated the Campeche female.

Distribution.—Texas south into Mexico in states bordering the Gulf of Mexico.

Material examined.—**MEXICO:** *Tamaulipas*: Llera Mesa (near summit), W98.59:N23.23, 16 April 1963, 1 ♀(?) 2 juv (W.J. Gertsch & W. Ivie, AMNH); *Campeche*: Chicanna ruins, ca. 8 km w Xpujil, ca. 89°31'W, 18°32'N, dead branch in short tropical rainforest, 12–14 July 1983, 1 ♀ (W. Maddison, MCZ).

Attidops cinctipes (Banks 1900),
NEW COMBINATION
Figs. 12–13, 24–28

Scius cinctipes Banks 1900:101 [*Scius a lapsus calami* for *Icius*]; Cotypes (2 ♀) from **USA: Louisiana**: Baton Rouge Parish, Baton Rouge, May (H. Soltaw, MCZ), examined, lectotype and paralectotype designated (subadult specimen also present)

Icius cinctipes: Banks 1910:71; Petrunkevitch 1911: 661; Bryant 1933:193, Figs. 42 (epigynum), 47(♀ dorsum); Roewer 1954:1222; Bonnet 1957: 2279

Ballus cinctipes: Edwards 1980:12 (n. comb.); Platinick 1993:738

Diagnosis.—As large to slightly larger than *A. youngi*, and the abdomen, while retaining remnants of the typical *Attidops* pattern (e.g., evidence of anterior pale spots and posterior light transverse bands), is dominated by pale coloration with symmetrical median dark maculations. Embolus with one and a half spirals, heavily sclerotized; embolus base sclerotized and extended dorsally to create shield with curved rectangular projection which cradles part of distal embolus. Epigynum with gonopores in two submedial, transverse slits; ducts like *A. cutleri* but larger.

Description.—Female CL 1.11 (1.18)–

1.30, CW 0.90 (0.95)–0.95, BL 2.45 (3.00)–3.10; male CL 1.21–1.40, CW 0.94–1.06, BL 2.50–2.90. Carapace brown, but lighter reddish-brown dorsally behind eyes and onto thoracic slope. Legs pale, with dark brown maculations dorsal distally on patellae, dorsal proximally on tibiae (in addition to broken proximal rings on tarsi and metatarsi), and laterally (both sides) on femora and tibiae; the femora may have one or two maculations each side. Dorsal abdominal pattern may coalesce into median chevrons, especially posteriorly, and there are many small dark spots laterally, approaching the pattern found in *Admestina*. Abdominal venter pale with median gray stripe flanked by several pair of gray spots.

Like *A. cinctipes*, the color pattern of *Admestina* consists of pale integument (except for the dark carapace) with dark maculations on legs and abdominal venter, and the pale abdominal dorsum has a series of connected dark median chevrons or triangles (more restricted to the sagittal plane and sometimes totally coalesced into a black median stripe) and small dark lateral spots, although the body is much narrower.

Distribution.—Florida to Louisiana, possibly into eastern Mexico (where two penultimate males with the appropriate color pattern were found); most found on laurel and water oaks.

Material examined.—**USA: Florida**: Alachua County, Gainesville, 7 February 1927, 1 ♀ (OSU); Lochloosa Wildlife Management Area, September–March, 1976–1985, 3 ♂ 21 ♀ (2 eggsacs with 3 and 5 eggs respectively) (G.B. Edwards, D.B. Richman; FSCA); Collier County, Royal Palm Park, March 1929, 1 ♀ (W.S. Blatchley, MCZ); Dade County, Homestead, 1 ♀ (AMNH); Highlands County, Lake Placid, Archbold Biological Station, 24 November 1961, 1 ♀ (A.M. Nadler, AMNH); Indian River County, Vero Beach, on *Avicennia germinans*, 10 July 1990, 1 juv (K. Hibbard & K. Dady, FSCA); St. Lucie County, on *Ficus* sp., 1 ♀ (E. Thompson & K. Hibbard, FSCA); **Louisiana**: Jefferson Parish, Harahan, 15 November 1944, 1 juv (E.G. Werner, MCZ); Tammany Parish, Covington, 1 ♀ (N. Banks, MCZ); **Mississippi**: Claiborne County, on car, 13 April 1954, 1 ♂ (H.K. Wallace, FSCA); **MEXICO**: *Tamaulipas*: nr. Gomez Farias, woody plants, 6 June 1983, 1 juv ♂ (W. Maddison, MCZ); *Veracruz*: Los Tuxtlas, dead palm fronds, 1 August 1983, 1 juv ♂ (W. Maddison, MCZ).

DISCUSSION

Maddison (1996) mentions both *Ballus* and *Admestina* among a group of genera possibly

derived from the Dendryphantinae. *Attidops* can be included in this group. All three genera have the embolus a distal spiral set perpendicular to the tegulum, an unequally bilobed tegulum, and the carapace integument is entirely reticulate (with coarser reticulations in the OQ extending past the PLE), which may be characteristic of the group. *Admestina* and *Attidops* share a flattened carapace with a long postocular dorsum; cusp-like flange subdistally on the anterior outer corner of male endites; the excavate cymbial tip and the transverse embolar groove; a broadly triangular epigynal plate; and the males have a complete dorsal abdominal scutum. *Ballus* has a small, subdistal anterolateral cusp on the male endites. Both the cusp and the flanges in this position might support a relationship to the dendryphantines (which have cusps), although not necessarily supporting a close relationship between *Ballus* and the two other genera. Marpissa (Marpissinae) is the only other genus with male endite cusps of which I am aware (D. Logunov, pers. comm.); further study may demonstrate the character has phylogenetic value.

Attidops cinctipes is the most distinct species in the genus; its color pattern and heavily sclerotized embolus are similar to *Admestina*, although otherwise it is like the other *Attidops* species. The embolus of *A. cutleri* is less sclerotized and its color pattern is intermediate between *A. cinctipes* and the *A. youngi*-*A. nickersoni* pair. The emboli of *A. youngi* and *A. nickersoni* are mostly membranous, and the epigyna are barely distinct; *A. nickersoni* is likely a Florida isolate of *A. youngi* and the two are sister species.

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A NEW *DISEMBOLUS* (ARANEAE, LINYPHIIDAE) FROM CAPE COD, MASSACHUSETTS AND LONG ISLAND, NEW YORK

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ABSTRACT. *Disembolus bairdi* new species is described from the coastal region of northeastern United States. Notes on the habitat, natural history and its associated spiders are provided.

The genus *Disembolus* is one of the groups of small erigonine spiders that are all too often described from single individuals with little or no information on their habitat or natural history. The genus is apparently found only in North America and was revised by Millidge in 1981, who recognized 22 species. The new species described here is common on the dunes adjacent to the salt and brackish water marshes of Cape Cod, Massachusetts and Long Island, New York.

Disembolus bairdi new species

Diagnosis.—Small spiders averaging 1.20 mm or less in total length. *Male:* Cymbium with stout knob engaging distal end of tibial apophysis; embolic spiral flat, large. Cephalic dome large and bulbous, sloped backwards, with sulci and pits. *Female:* Epigynum with broad mantle, posterior plate hyaline, with oval, bubble-like bilateral areas, spermathecae widely spaced.

Etymology.—The species is named after Spencer F. Baird, who played the principal role in selecting Woods Hole, Massachusetts, as a center for marine research, and was the first director of the U.S. National Museum.

Material examined.—Holotype male, allotype female and 24 paratype males and 29 paratype females, collected 23 December 1985 and 22 December 1986, under storm tide debris, West Falmouth Harbor, West Falmouth, Barnstable County, Massachusetts. Additional specimens collected at the same locality: five adult females, 14 April 1990, eight adult females, 9 May 1989, and one adult male, 10 October 1990. A gravid female was collected 22 April 1990, in brackish marsh debris, Salt Pond, Falmouth. All above material

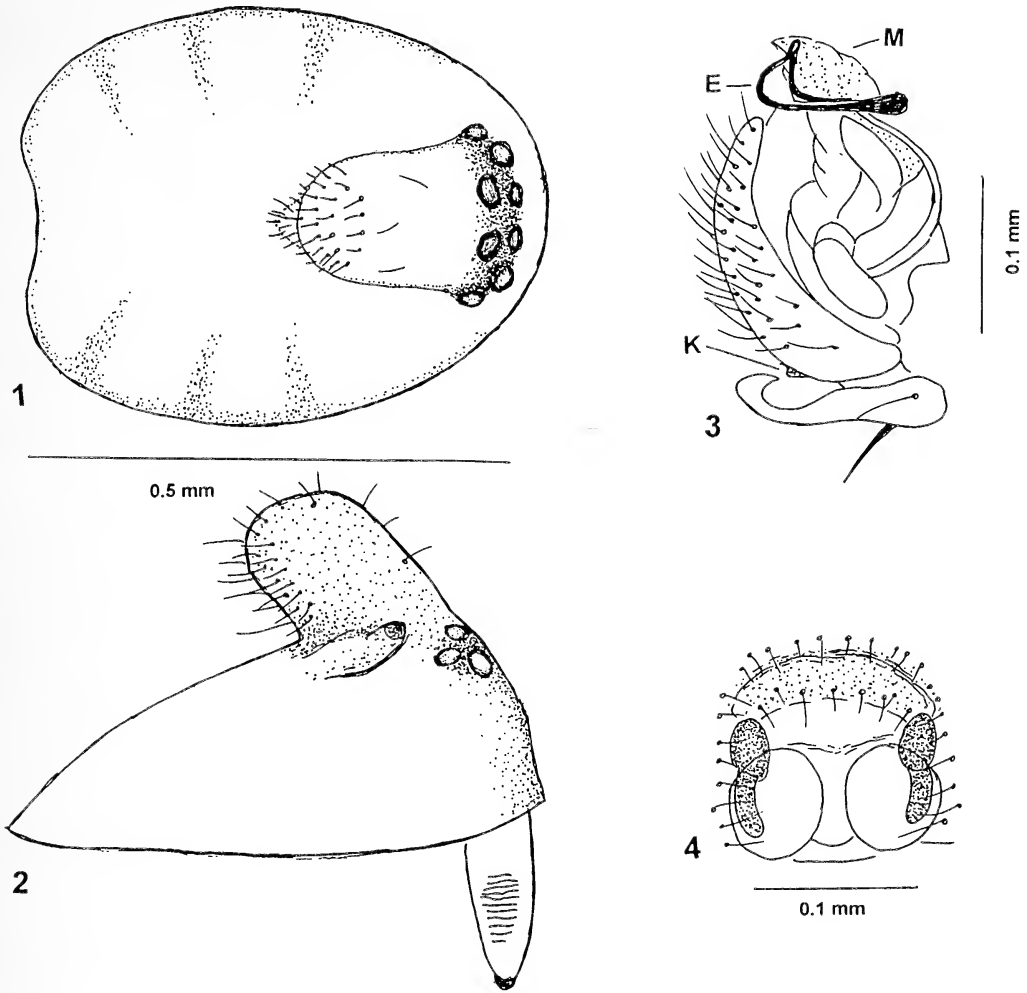
was collected by R.L. Edwards. In December 1995, and in April and May 1996, Miss Jacqui Kluft collected adult male and female and pre-mature specimens in detritus at storm tide levels on the beach at Fire Island, New York.

Holotype male and allotype female, paratype males and females deposited in the United States National Museum, Washington, D.C.; paratype males and females in the Museum of Comparative Zoology, Cambridge, Massachusetts, in the American Museum of Natural History, New York and in the British Museum of Natural History, London.

Measurements were made with an ocular micrometer. The cephalic index is the length of the cephalothorax divided by the width. The TmI value is the ratio of the length of metatarsus I divided by the distance between the trichobothrium and the proximal end of the metatarsus.

Description.—Measurements (mm), means in mm and SD. *Female:* ($n = 12$). Total length 1.20 ± 0.057 , cephalothorax length 0.51 ± 0.031 , cephalic index 1.29 ± 0.082 , TmI 0.49 ± 0.022 , epigynum width 0.16 ± 0.009 . *Male:* ($n = 12$). Total length 1.17 ± 0.053 , cephalothorax length 0.53 ± 0.036 , cephalic index 1.24 ± 0.061 , TmI ratio 0.47 ± 0.024 , TmIV absent. Tibia without spines in male, in female 0-0-1-1.

Cephalothorax broad, light yellow-brown with thin, dark margin. Clypeal area and dome slightly darker. Eyes margined with black. Vague radii on thoracic portion but otherwise without distinctive markings (Fig. 1). Male with large dome on cephalic portion of cephalothorax, sloped to the rear (Fig. 2). Large sulcus at base of lobe with pit immediately behind posterior lateral eye. Chelicera with



Figures 1-4.—*Disembolus bairdi* new species. 1, Male cephalothorax, dorsal; 2, Male cephalothorax, lateral; 3, Left palp, ectal. Note the apparent conjunction of the distal tip of the tibial apophysis and the knob on the cymbium; 4, Epigynum, ventral. Abbreviations: E, embolus; K, knob-like process on cymbium; M, supratergular apophysis, membranous part.

four promarginal teeth, two retromarginal. Abdomen grey to black, rarely with indistinct chevrons on posterior half, venter lighter. Sternum with darker margin. Legs light yellow-orange. Palp (Fig. 3) with broad, relatively flat base of the embolus spiral with a recurved distal loop and projecting fan-like membranous supratergular process (Fig. 3). Cymbium with stout, darkened knob-like process that engages distal end of tibial apophysis (Fig. 3). Palpal tibia with a single trichobothrium, a stout seta, and recurved distal tip. Female cephalothorax without dome, colored essentially as male. Epigynum with broad, darker

mantle anteriorly (Fig. 4). Posterior plate glassy, with bilateral swellings. Spermathecae widely spaced, clearly visible. Spermathecal ducts not clearly visible.

Millidge (1981) provided partial keys for the males and females of *Disembolus*. For females (table 1), *D. bairdi* new species fits best under line 4, "with posterior plate notably convex and glassy in appearance, and with dark colored bar anterior to plate." For males (table 2), *bairdi* new species fits best under line 3, "Carapace with a lobe which has a hole and sulcus on each side," and under line 3-iv, "tibial apophysis with small hook distally." It

will be noticed that *D. bairdi* new species is much smaller (± 1.2 mm) than the species listed in this line.

Natural history.—This species is found under mats of organic debris without obvious webbing, usually *Zostera* and/or *Spartina*, found at or near the highest tide levels in areas otherwise protected from direct ocean influence. The spider occupies the interface between these mats and the underlying sand. When the mats are lifted the spiders will sometimes burrow into the sand. Immature instars were taken in March, September and October, with most individuals mature in December. Mature females have been taken through May. Apparently most of the species of this genus are found in the colder months of the year (Millidge 1981). It shares the highest tidal zone habitat with *Colonus americana* Chamberlin & Ivie 1944, another erigonine species that matures in the late fall. *Colonus* was as abundant as *Disemboolus bairdi* in the West Falmouth Harbor area and was also found by Miss Jacqui Kluft on Long Island with *D. bairdi* and *Erigone brevidentata* Emerton. *Erigone aletis* Crosby & Bishop 1928, and *Grammonota trivittata* Banks 1895 were also abundant in or on detrital mats on Cape Cod. These species also mature during the colder months of the year. Two additional species of *Disemboolus* occur on Cape Cod. *Disemboolus sacerdotalis* (Crosby & Bishop

1933) has been taken in grassy areas in mixed woodlands and several females of an apparently undescribed species have been taken in pine litter.

Millidge (1981) notes the difficulty in seeing the transparent spermathecal ducts of *Disemboolus* species. In *D. bairdi*, they are virtually invisible, even in prepared material. Three epigyna were removed and mounted in a lactic-acetic acid mixture, PVA, and euparal. In PVA mounted material what appeared to be wide-mouthed spermathecal ducts could be discerned only with considerable uncertainty. Histological preparations may be necessary to fully describe the internal genitalia of *Disemboolus* species.

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Dr. Charles Dondale and Mr. James Redner, Research Branch, Agriculture Canada, examined my specimens and confirmed my opinion that this was an undescribed species. Eric Edwards kindly critiqued the draft manuscript. Comments and corrections provided by reviewers were much appreciated.

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SINOPODA, A NEW GENUS OF HETEROPODINAE (ARANEAE, SPARASSIDAE) FROM ASIA

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ABSTRACT. *Sinopoda* new genus (Araneae, Sparassidae, Heteropodinae) is described from Asia. It is recognizable only from genital characters. At present, the new genus comprises 25 species from Japan, Korea, China, Thailand, Malaysia and east India. *Heteropoda campanacea*, *H. forcipata*, *H. hamata*, *H. koreana*, *H. licenti*, *H. marsupia* (?), *H. minschana*, *H. serrata*, *H. shennonga*, *H. stellata* and *Panaretidius microphthalmus* are placed in *Sinopoda* new genus. Relationships to other heteropodine genera are discussed.

Jäger (1998a) identified somatic characters, which are useful for distinguishing suprageneric taxa in the Sparassidae. At present, nine heteropodine genera are known from Asia: *Adrastis* Simon 1880, *Heteropoda* Latreille 1804, *Panaretidius* Simon 1906, *Panaretus* Simon 1880, *Pandercetes* L. Koch 1875, *Parhedrus* Simon 1887, *Spariolenus* Simon 1880, *Torania* Simon 1886, *Yiinthei* Davies 1994. Most of the species belonging to *Sinopoda* new genus were formerly described under *Heteropoda*.

METHODS

The following abbreviations are used in the text: AC, anterior width of carapace; AL, abdomen length; ALE, PME, AME, PLE, ME, LE, AE, PE refer to anterior lateral eyes, posterior median eyes, etc.; AW, abdomen width; BL, body length; CH, carapace height; CL, carapace length; CW, carapace width; GL, gnathocoxae length; GW, gnathocoxae width; LL, labium length; LW, labium width; mm, millimeters; n, number of examined specimen; SL, sternum length; SW, sternum width. NHMB, Naturhistorisches Museum Basel, NHMW Naturhistorisches Museum Wien, SMF Senckenberg Museum Frankfurt, ZMB, Zoologisches Museum der Humboldt-Universität Berlin.

Spine notation follows Davies (1994), exceptions are given in brackets. Dissected epigyna were cleared in lactic acid. Measurements are in mm. The variation of measurements is given first, followed by measurements of the lectotype in brackets.

For characterizing the new genus and giving

information of its distribution, 14 undescribed species were examined, which are recognized by the author as species of *Sinopoda* new genus.

SYSTEMATICS

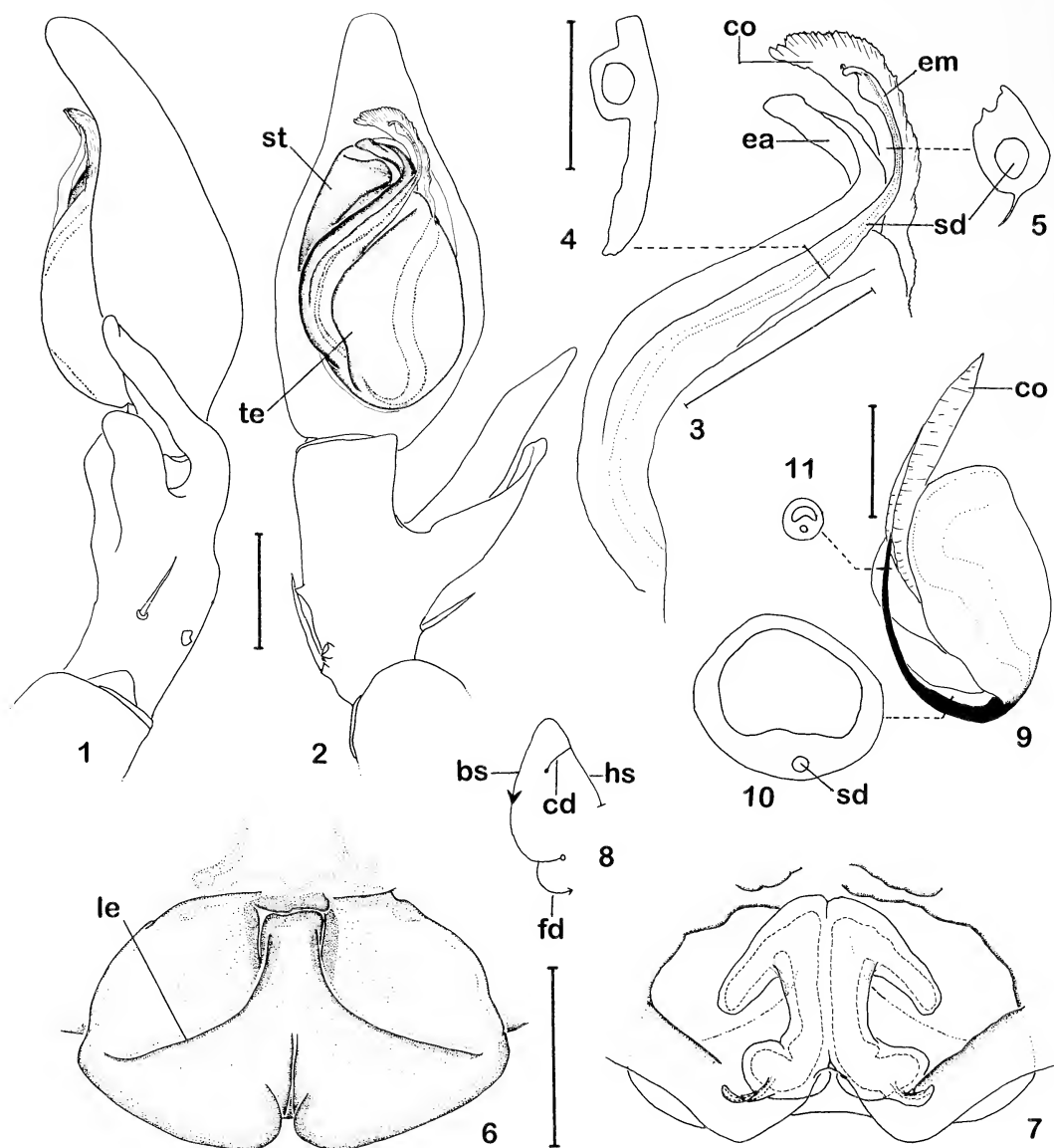
***Sinopoda* new genus**

Type species.—*Sarotes forcipatus* Karsch 1881.

Diagnosis.—Close to *Heteropoda* but male palps with embolic apophysis. Conductor membranous, arising from the distal part of the tegulum (Figs. 2, 3). Tibial apophysis bifurcate, dorsal branch longest (Fig. 1). Copulatory ducts of vulva uncoiled, running from anterior genital orifice to posterior part of spermathecae. Typically they are fused along the median line (Fig. 7). Spermathecae divided into a basal part and a head, situated laterally from the entrance of the copulatory duct into the spermathecae (Fig. 8).

Etymology.—The name is an acronym of the prefix *sino-* (belonging to China) and *Heteropoda*. The gender is feminine.

Characters of checked *Sinopoda*-species.—Small to large spiders (3–25 mm) with laterigrade legs. *Carapace*: widest above coxa II to III; CL/CW 1.0 to 1.3; CW/AC in ♂ 1.8–2.3, in ♀ 1.4–1.8; fovea and highest point of carapace mostly above coxa III; CL/CH 2.7–6.2. Sternum broadest between coxa II; SL/SW 0.9–1.1 (0.9 = BL < 6mm). LW/LL 0.9–1.3 (BL > 8mm), 1.3–1.7 (BL < 6mm). GL/GW 1.5–2.4. *Abdomen*: oval, AL/AW 1.2–3.3 (mean 1.7; n = 24). *Eyes*: in two rows, viewed from above both rows recurved. *Chelicerae*: with 3 anterior and 4



Figures 1–11.—1–8. Genital characters of paralectotypes of *Sinopoda forcipata* NEW COMBINATION from Japan. 1. Lateral aspect of left palp; 2. Ventral aspect of left palp; 3. Ventral aspect of embolus and conductor; 4, 5. Cross sections of embolus; 6. Ventral aspect of epigynum; 7. Dorsal aspect of vulva; 8. Schematic course of right spermatheca; 9–11. Male genital characters of *Heteropoda venatoria* Linnaeus: 9. Ventral aspect of tegulum; 10, 11. Cross sections of embolus. Abbreviations: Bs, Basal part of spermathecae; cd, copulatory duct; co, conductor; ea, embolic apophysis; em, embolus; fd, fertilization duct; hs, head of spermathecae; le, ledges of epigynum; sd, sperm duct; st, subtegulum; te, tegulum. Scales for Figs. 1–3, 6, 9 = 1.0 mm; Figs. 4, 5, 10, 11 = 0.1 mm.

posterior teeth and several denticles in between them; as in all other heteropodine species majority of denticles near the anterior teeth (Jäger 1998a). *Legs*: length in most cases 2143 ($n = 24$), also 2413 ($n = 7$), 2431 ($n = 3$), 2134 ($n = 2$). In cavernicolous spe-

cies and in all males legs, especially tibiae and metatarsi, elongated relative to body length. Scopulae on tarsi and distal part of metatarsi, sparse in some species. Palpal claw in females present, with 5 to 11 long teeth. *Color*: variable, pale brown and pale yellow

in cavernicolous species to dark brown, with or without pattern.

Male palp: Part of subtegulum visible in ventral view. Tegulum oval in general shape. Embolus more or less s-shaped, arising from prolateral part of tegulum in a 6 to 8 o'clock position, basally embedded in a tegular flange (Fig. 2). Tip of embolus near membranous and flattened conductor (Fig. 3). Embolus broadened, containing just one cavity (sperm duct) as in *Sinopoda forcipata* NEW COMBINATION (Figs. 4, 5), some species with tooth in subdistal position. Embolic apophysis arising prolaterally from the basal half of the embolus, embedded distally in a subtegular furrow. By comparison, embolus of *Heteropoda* filiform, not s-shaped (Fig. 9) and with two tubuliform cavities, a narrow sperm duct and a large one, which is connected with the tegular cavity (Figs. 10, 11). Conductor thicker, sheath-like, tapering and arising on a prolateral position of tegulum (Fig. 9).

Epigynum: Characterized by copulatory orifices covered by two ledges running from a medio-anterior to latero-posterior position. Two posterior lobes in some species divided in the median line. The darkened field of epigynum sometimes extended in two anterior elongated bands, these sometimes separated from epigyneal field (Fig. 6). In *Heteropoda* rims aligned in direction of body axis, in most cases short. Copulatory ducts coiled, if touching each other then only at their origin.

Distribution.—Japan, Korea, China, Thailand, Malaysia (Selangor, Sarawak), east India (Assam).

Natural history.—Little is known about the representatives of this genus. Deeleman (1998) collected specimens in Borneo (W-Sarawak, Matang reserve) from tree bark and grass. The author observed individuals in China (Shaanxi, Taibai Shan) in leaf litter, running like lycosids during the day. Another species there inhabited natural rock fissures and man-made walls. This species came out at a certain time in the evening to ambush for prey always near the same spot (Jäger 1998b). Other species are reported from caves, though not all of them appear to be restricted to caves.

Other species included in *Sinopoda*.—*Sinopoda campanacea* (Wang 1990) NEW COMBINATION, *S. hamata* (Fox 1937) NEW COMBINATION, *S. koreana* (Paik 1968) NEW COMBINATION, *S. licenti*

(Schenkel 1953) NEW COMBINATION, *S. marsupia* (Wang 1991)(?) NEW COMBINATION, *S. minschana* (Schenkel 1936) NEW COMBINATION, *S. serrata* (Wang 1990) NEW COMBINATION, *S. shennonga* (Peng, Yin & Kim 1996) NEW COMBINATION, *S. stellata* (Schenkel 1963) NEW COMBINATION, *S. microphthalma* (Fage 1929) NEW COMBINATION.

Sinopoda forcipata (Karsch 1881) NEW COMBINATION

(Figs. 1–8)

Sarotes forcipatus Karsch 1881:38. (Syntypes: 3♂ (ZMB 2696, 2698/2), 2♀ (ZMB 2694, 2695), 1♀ with epigynum region dissected (epigynum is missing) and a subadult ♂ (both ZMB 2696) - labeled: Japan, leg. Hilgendorf, det. Karsch -, examined. 1♂ (ZMB 2698, both palps and legs entire, PJ 921) hereby designated as lectotype, others as paralectotypes)

Heteropoda forcipata: Bösenberg & Strand 1906: 276; Järvi 1912:82, 113; 1914:209; Fox 1936: 127; 1937:7; Suzuki 1952:3, 14; Roewer 1954: 714; Bonnet 1957:2189; Yaginuma 1960:113; 1962a:52; 1962b:75; 1962c:130; 1963:51; 1971: 113; 1975:190, 1986:199; Chikuni 1989:130; Yaginuma 1990:270; Ono et al. 1995:128.

Diagnosis.—Male with distal part of embolic apophysis bent at a right angle (Figs. 2, 3); dorsal branch of tibial apophysis broad and tapering (Fig. 1). ♀ posterior lobes of epigynum point towards the median line, closest distance between ledges about 1/5 of total width of epigynum (Fig. 6); head of spermathecae two times as long as broad, nearly constant in width (Fig. 7).

Redescription of male.—CL 7.3–9.8 (9.1), CW 6.4–8.8 (7.9), AC 3.4–3.9 (3.7), CH 1.5–2.4 (1.9), AL 8.0–11.0 (10.2), AW 4.7–6.3 (5.5). **Color:** Pale yellowish-brown, without distinct pattern. **Eyes:** Diameters AME 0.30–0.44, ALE 0.41–0.53, PME 0.34–0.41, PLE 0.45–0.53, interdistances AME-AME 0.22–0.27, AME-ALE 0.07–0.12, PME-PME 0.33–0.47, PME-PLE 0.52–0.58, AME-PME 0.44–0.49, ALE-PLE 0.36–0.47, clypeus AME 0.41–0.55, clypeus ALE 0.40–0.62; both rows recurved in dorsal view. **Legs and palps:** 2143 (measurements see Table 1). **Spinination:** Palps 131, 101, 211(small/0)1. Femora I-II 323, III 333, IV 331. Patellae 101. Tibiae 2326. Metatarsi I 102(1)4, II 1(2)01(2)4, III 2026, IV 3036.

Table 1.—Leg and palp measurements in males (*n* = 8) of *Sinopoda forcipata* NEW COMBINATION.

Leg segment	Palp	I	II	III	IV
Femur	4.3–5.1	10.1–12.0	11.0–13.6	9.1–11.1	9.6–11.8
Patella	1.5–2.4	3.5–5.0	3.8–5.0	2.7–4.3	3.1–4.1
Tibia	2.4–2.9	11.0–13.0	12.1–14.2	8.8–10.7	9.7–11.5
Metatarsus	—	10.8–13.8	12.5–15.4	8.8–10.8	10.6–12.7
Tarsus	3.6–4.3	3.5–4.0	3.9–4.5	2.7–3.5	3.4–3.6
Total	11.8–14.7	39.0–47.1	53.3–52.4	32.6–39.1	36.7–43.1

Female.—CL 9.7–10.2, CW 8.2–8.8, AC 4.9–5.3, CH 2.4–2.6, AL 10.6–13.9, AW 6.0–8.3. *Color:* As in male. *Eyes:* Diameters AME 0.29–0.44, ALE 0.48–0.55, PME 0.37–0.42, PLE 0.51–0.58, interdistances AME–AME 0.28–0.42, AME–ALE 0.10–0.22, PME–PME 0.48–0.55, PME–PLE 0.63–0.77, AME–PME 0.54–0.67, ALE–PLE 0.58–0.63, clypeus AME 0.63–0.74, clypeus ALE 0.56–0.69. *Legs and palps:* 2143 (measurements see Table 2). *Spination:* Palps 131, 1(0)01, 2121, 1014. Femora I–III 3(4)2(3)3(2/4), IV 33(2)1(2). Patellae 101. Tibiae I–II 22(0/1)26, III–IV 23(1/2)26. Metatarsi I–II 1014, III 2014(2016/2026), IV 3036. Palpal claw with 7–8 teeth.

Other material examined.—3♂2♀ (NHMB 551, labeled: Clubionidae, *Heteropoda aulica* (L. K.), Japan, Yokohama, G.v.R. Merian), 1♀ (ZMB 2396, labeled: *Sarotes aulicus* L. Koch. Nagasaki Westrh.), 1♂ (SMF 4578, labeled: *Heteropoda invicta* (L. Koch), 1♂, Japan: Saga, W. Dönitz S.), 1♂ (SMF 4595, labeled: Eusparassid No. 41, *Heteropoda forcipata* (Ka.), 1♂, China, Roewer det. 1933), 1♂ (NHMW 1879.II.20, labeled: holotype of *Heteropoda invicta*, Inv.-No. 17.863, Coll. Musei Vindobonensis, *Sarotes invictus*, Erber Tausch).

Note.—In Japan two species exist, *Sinopoda forcipata* NEW COMBINATION and *S. stellata* NEW COMBINATION. The descrip-

tions by L. Koch (1878) of *Heteropoda aulica* and *H. invicta* have caused some problems. Individuals of *S. forcipata* NEW COMBINATION have been examined by the author, which were determined as *H. aulica* or *H. invicta*. *H. aulica* clearly does not belong to *Sinopoda* new genus. *H. invicta* cannot clearly be recognized from the original description. There are two specimens deposited in NHMW in one vial, which are labeled as 'holotype', one male and one female. Koch described only one female. The female belongs to *Heteropoda venatoria* Linnaeus 1767, the male to *Sinopoda* sp. The original drawing No. 32 by Koch does not permit a clear association with this genus. If the species belongs to *Sinopoda* new genus, the epigynum is turned upside down.

Color variation.—In most other specimens examined color dark yellow to brown.

Distribution.—Japan, China.

DISCUSSION

Autapomorphic characters of the new genus are: embolic apophysis, bifurcate tibial apophysis, and course of epigyneal rims. The shape of the conductor resembles that of *Barylestis* (Africa), *Pandercetes* (Asia, Australia), *Spa-riolenus* (Asia) and two undescribed genera from Asia. In contrast to them, *Heteropoda*

Table 2.—Leg and palp measurements in female (*n* = 5) of *Sinopoda forcipata* NEW COMBINATION.

Leg segment	Palp	I	II	III	IV
Femur	4.0–4.6	9.5–10.4	10.6–11.5	9.1–10.3	9.7–10.8
Patella	2.1–2.3	4.4–4.9	4.6–4.9	3.8–4.2	3.7–3.9
Tibia	2.8–3.3	10.0–10.6	10.2–11.2	8.1–9.3	8.8–9.7
Metatarsus	—	9.0–9.5	9.1–10.0	7.3–8.4	9.0–9.8
Tarsus	4.1–4.5	2.8–3.1	2.8–3.0	2.1–2.9	2.2–3.1
Total	13.0–14.4	36.9–38.4	36.8–40.5	30.9–34.8	34.2–37.3

(all continents) and *Parhedrus* (Asia) possess sheath-like conductors. Järvi (1912, 1914) recognized the female genital organs of *S. forcipata* NEW COMBINATION as an extreme specialization and stated that in a hypothetical ancestral epigynum the lateral lobes and the ducts were medially fused. This conclusion can be confirmed, as in several species a median furrow is present. Furthermore, he homologized the head of spermathecae of *Sinopoda forcipata* NEW COMBINATION with the coils in *Heteropoda* spp., which is here rejected. In *Heteropoda* spp. the head of the spermathecae is absent. As *S. forcipata* has uncoiled ducts with a simple cavity, it is supposed that this type of vulvae has been divided from *Heteropoda* s. str. and other heteropodine genera a relatively long time ago. The most primitive species of *Sinopoda* new genus is known from W-Sarawak (Borneo). The typical epigyneal ledges of *Sinopoda* spp. are homologous with those of *Heteropoda* spp., but in the latter genus they either are covered by the lateral lobes or are situated in the anterior part of the epigynum. For these reasons, I consider *Sinopoda* new genus a monophyletic group, whose exact placement within the Heteropodinae is not yet clear. To elucidate intergeneric relationships more taxa need to be examined.

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**CARBINEA, A NEW SPIDER GENUS
FROM NORTH QUEENSLAND, AUSTRALIA
(ARANEAE, AMAUROBIOIDEA, KABABININAE)**

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ABSTRACT. The distribution of four species of *Carbinea* new genus in the Wet Tropics region of northern Queensland documents the species' richness and local endemism. The new species are *C. longiscapa*, *C. breviscapa*, *C. wunderlichi* and *C. robertsi*. They are placed in the sub-family Kababininae which is removed from the Amphinectidae (Davies 1995) as there is evidence that it does not belong there. The placement of this clade remains problematical.

Amaurobioid spiders abound in Australia. In rainforest surveys (Monteith & Davies 1984) they were usually found to have the highest number of species after 'theridiids' and salticids. From the number of identifiable species in these surveys it was estimated that probably less than 20% of the Australian spiders are described. At present about 40 amaurobioid genera are known; however, their placement in families is unresolved. In describing *Kababina* (Davies 1995) I said that it belonged in a group of undescribed genera. One of these genera is ecribellate and is described here.

METHODS

Spiders were collected from rainforests in the Wet Tropics region of North Queensland between latitudes 16°16'S, 17°06'S. All material is deposited in the Queensland Museum (QM Brisbane, Australia). Measurements are in millimeters. Coordinates are given in square brackets when these were not included in the original label data. Lengths of epigynal scape, cymbium and tibial apophysis were measured by linear micrometer on a dissecting microscope and converted to millimeters. Length of the epigynal scape was measured from the posterior edge of the fossa. Notation of spines follows Platnick & Shadab (1975). Illustrations were drawn with the aid of a camera lucida. The left male palp is illustrated.

Collection methods include litter-sieving

followed by heat extraction in funnels, pit-fall (PF) collection, pyrethrum (PY) spraying of tree-trunks and fallen logs, hand collecting from under logs in daylight and night collecting. Most spiders were collected by G.B. Monteith (GBM) and fellow collectors D. Cook (DC), D. Yeates (DY), G. Thompson (GT), H. Janetzki (HJ), L. Roberts (LR) and the Australian New Zealand Scientific Exploration Society (ANZSES). Table 1 lists anatomical abbreviations used in Table 3 and the text; abbreviations on illustrations are explained in the legends to figures.

SYSTEMATICS

Subfamily Kababininae

Diagnosis.—Three-clawed spiders. Coloration of the abdomen varies from pale to dark grey-black with pattern of light spots in vague chevron pattern. Carapace highest in foveal region (Fig. 1); eyes directed forwards (Fig. 2). Posterior eye row straight or slightly recurved, anterior row straight (Fig. 3); AME reduced. Two retromarginal and two promarginal cheliceral teeth (Fig. 5); prolateral filamentous seta at base of fang longer than other setae. Labium about as long as wide; sternum slightly longer than wide, pointed posteriorly (Fig. 6). Legs 1423/4123. Feathery hairs on legs (Fig. 24). Tarsal trichobothria increasing in length distally; bothrium collariform (Fig. 25). Tarsal organ slit-like, broadening distally. Epigynum with medial

Table 1.—List of anatomical abbreviations.

AL	abdomen length
ALE	anterior lateral eyes
ALS	anterior lateral spinnerets
AME	anterior median eyes
APOPH	apophysis
AW	abdomen width
CB	cymbium
CH	cheliceral
CL	carapace length
CR	cribellum
CW	carapace width
E	embolic
EPIG	epigynal
MAP	major ampullate spigots
MT	metatarsal
PCR	paracribellar spigots
PLE	posterior lateral eyes
PME	posterior median eyes
PLS	posterior lateral spinnerets
PMS	posterior median spinnerets
RTA	retrolateral tibial apophysis
TRICH	trichobothria

fossa wider than long (Fig. 8); spermathecae posterior (Fig. 9) or lateral to fossa. Male palp with rounded tegulum (Fig. 16); course of sperm duct showing clearly. Membranous conductor; embolus with or without proximal embolic apophyses; without median apophysis. Tibial apophysis with ventral and dorso-retrolateral branches (Fig. 17). Cribellum (two fields) present or absent in females, absent in males; proximal calamistrum with one row of setae. Large broad colulus (Figs. 4, 41) when cribellum is absent. Anterior spinnerets largest with short conical terminal segment; two major ampullate spigots on female ALS; one and a nubbin on male ALS. Posterior spinnerets with long slender terminal segment.

Carbinea new genus

Type species.—*Carbinea longiscapa*

Etymology.—The generic name is from the Carbine Tableland, north Queensland, the geographic area where three species have been collected.

Diagnosis.—Ecribellate (cf. *Kababina*) spider. The epigynum has a long, medium or short posterior scape. The embolus and conductor arise antero-ventrally on the tegulum; the embolus has two elaborate brush-like apophyses (cf. *Kababina*) proximally.

KEY TO *CARBINEA* SPP.

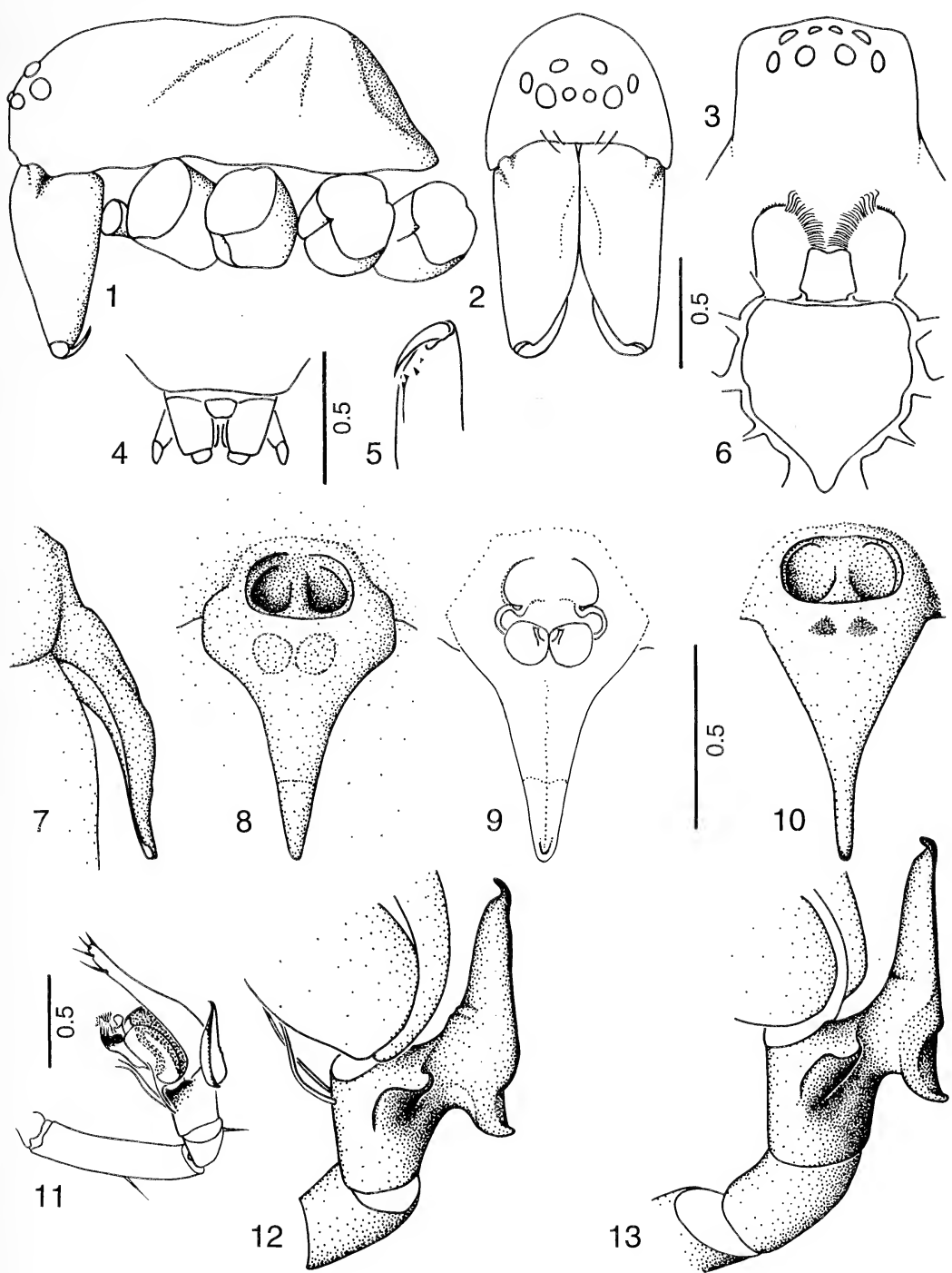
- 1. Posterior epigynal scape medium to long, 0.4–0.7; ♂ tibial apophysis half or more than half the length of cymbium 2
- Posterior epigynal scape short, 0.3–0.4; ♂ tibial apophysis a third or less the length of cymbium 3
- 2. Epigynal scape very long, 0.6–0.7. Tibial apophysis more than half the length of the cymbium *longiscapa*
- Epigynal scape medium length (0.4). Tibial apophysis about half the length of the cymbium *robertsi*
- 3. Epigynal scape short (0.3). Tibial apophysis short, thick without heel . . . *breviscapa*
- Epigynal scape medium (0.4). Tibial apophysis with heel *wunderlichi*

Carbinea longiscapa new species

(Figs. 1-13, 22, 23, 42, 43. Tables 2, 4)

Types.—**Australia:** *North Queensland.*

Holotype ♀, Stewart Ck., 4 km NNE Mt. Spurgeon, Carbine Tableland, Camp 1, 16°24'S, 145°13'E, 1250–1300 m, 15–20 October 1991, GBM, HJ, DC, LR (QM S30283). Paratypes: ♂, same data as holotype (S30284); 4♂, PF (S30285); ♀, ♂ (S30286); ♂ (S30287); 4♂, PF (S30288); 2♀, 7 km N Mt. Spurgeon, Camp 2, 16°22', 145°13', 1200–1250 m, 17–19 October 1991; GBM, HJ, DC, LR (S30289); ♀, ♂, PF (S30290); 2♀, ♂, PF (S30291); ♀ (S30292); 2♀, Upper Whyanbeel Ck, 16°23', 145°17', 150 m, PY, 5 September 1992, GBM (S35247); ♀, Black Mtn., 4.5 km N Mt. Spurgeon, 16°24', 145°12', 1240 m, PY, 17 October 1991, GBM, HJ (S35223); 2♂, Karnak-Devils Thumb, 16°24', 145°18', 8–12 km NW Mossman, 1120 m, PF, 26 December 1989–15 January 1990, ANZSES (S35231); 2♂, 16°23', 145°17', 1080 m, PF (S35232); ♀, ♂, Stony Ck., 2.5 km NE Mt. Spurgeon, 16°25', 145°13', 1200 m, 15–21 October 1991, PF, GBM, HJ, DC, LR (S30294); ♂, Head of Roots Ck., 12 km WNW Mossman 16°24', 145°15', 1200 m, PF, 28 December 1989–11 January 1990, ANZSES (S35230); ♀, Upper Cow Ck., 1.5 km NE Mt. Spurgeon, 16°26', 145°13', 1180 m, 15–21 October 1991, PF, GBM, HJ, DC, LR (S30293); ♀, 2♂, Pauls Luck, 16°26', 145°15', 1100 m, PF, 28–30 November 1990, GBM, HJ, DC (S35224); ♀, 2 km SE Mt. Spurgeon via Mt. Carbine 16°27', 145°12', 1100 m, 20 December 1988, PY, GBM, GT (S30295); ♀, 20 De-



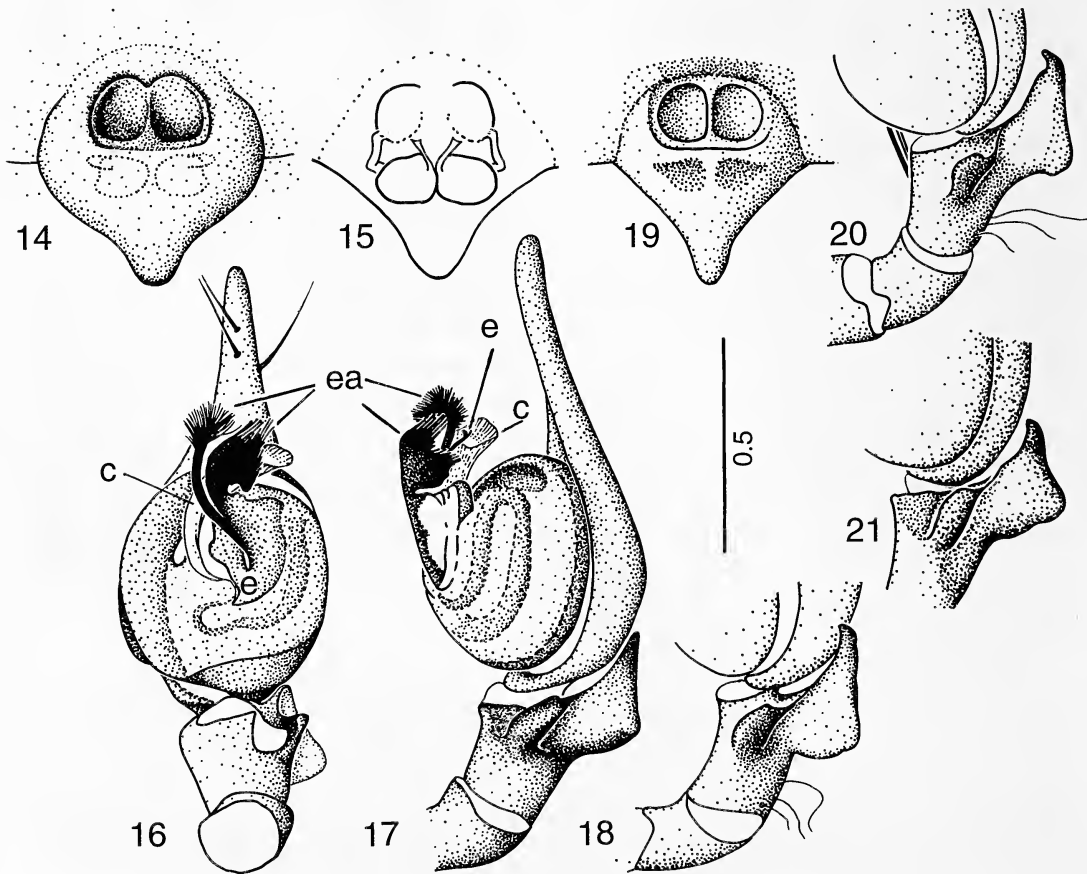
Figures 1-13.—*Carbinea longiscapa* new species. 1-10, Female. 1, Cephalothorax, lateral view; 2, Eyes, chelicerae, frontal view; 3, Eyes, dorsal view; 4, Colulus, spinnerets; 5, Chelicera; 6, Endites, labium, sternum; 7-9, Epigynum, lateral, ventral, dorsal views; 10, Epigynum (Mossman Bluff); 11-13, Male. 11, Palp; 12, Tibial apophysis; 13, Tibial apophysis (Mossman Bluff).

Table 2.—Leg lengths of ♀(♂) *Carbinea longiscapa* new species.

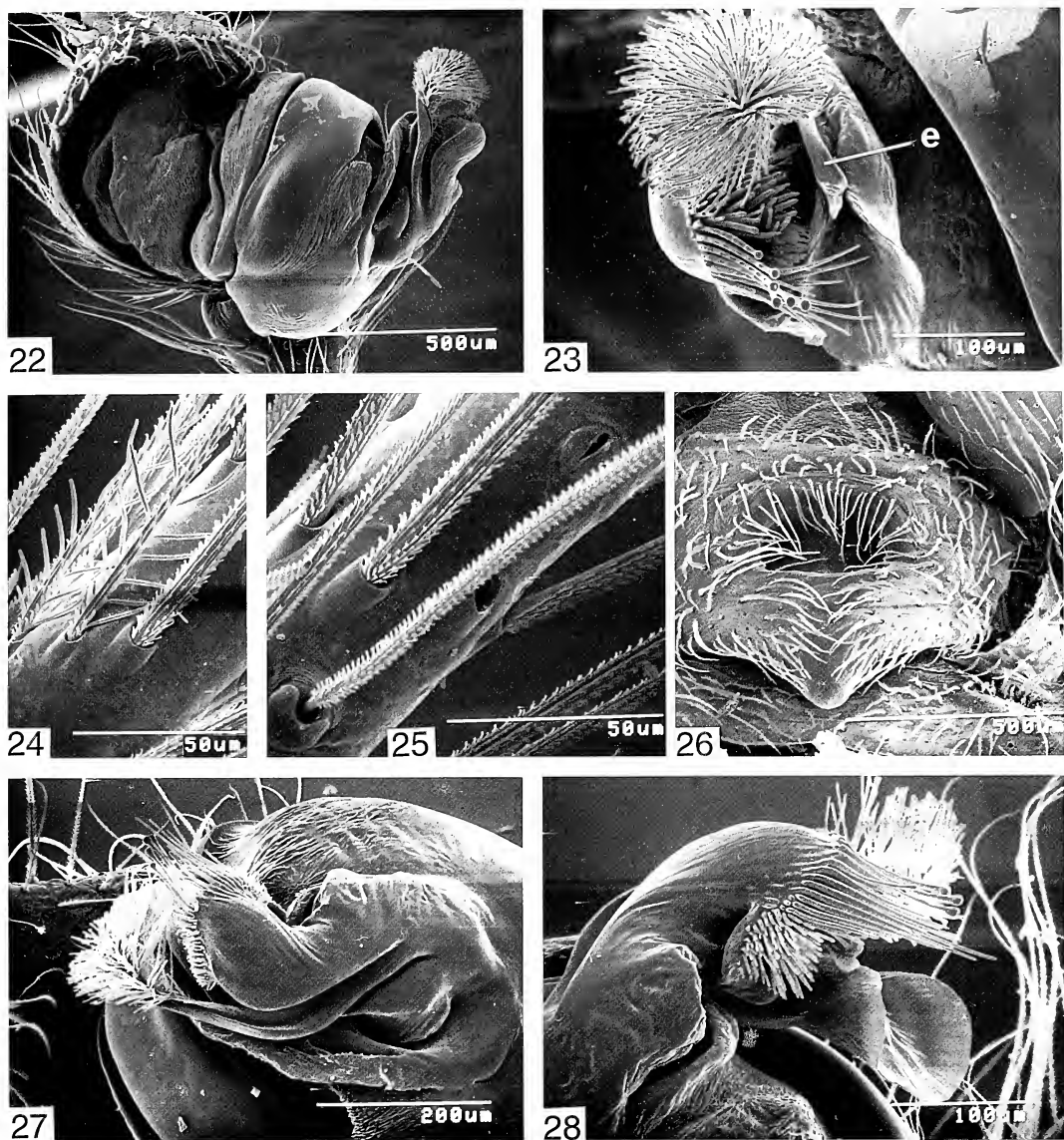
	Leg I	Leg II	Leg III	Leg IV
Femur	2.1 (2.3)	1.7 (1.8)	1.5 (1.7)	2.0 (2.2)
Patella	0.6 (0.6)	0.6 (0.6)	0.5 (0.5)	0.6 (0.6)
Tibia	2.1 (2.2)	1.4 (1.5)	1.3 (1.2)	2.0 (2.1)
Metatarsus	2.0 (2.4)	1.5 (1.7)	1.5 (1.6)	2.1 (2.4)
Tarsus	1.3 (1.3)	1.0 (1.0)	0.9 (0.9)	1.2 (1.2)
Total	8.1 (8.8)	6.2 (6.6)	5.7 (5.9)	7.9 (8.5)

cember 1988–4 January 1989, GBM, GT, ANZSES (S35222); ;2fe, ♂, 9 km W. Mossman, 16°28', 145°16', 1000 m, PY, 22 December 1989, GBM, ANZSES (S35229); ♀, 10 km W Mossman, 1100–1300 m, 17–18 December 1988, GBM, GT (S16540); 2 ♀, Mossman Bluff Camp, 16°28', 145°17', 1000 m, PF, 30 November 1990, GBM, HJ

(S35226); ♂, Mossman Bluff Track, 5–10 km W Mossman, 1180 m, PF, 1–17 January 1989, GBM, GT, ANZSES (S27724); ♂, 17–31 December 1988, (S35227); ♂, 10 km W Mossman, 1200 m, PY, 17 December 1988, GBM, GT (S35228); ♀, ♂, Mt. Demi summit, 16°30', 145°19', 1000 m, PY, 16–17 December 1995, GBM (S35225); ♀, Upper



Figures 14–21.—*Carbinea breviscapa* new species. 14–15, Epigynum, ventral, dorsal 16–17, Male palp, ventral, retrolateral; 18, Tibial apophysis; 19–20, from Black Mountain; 19, Epigynum; 20, Tibial apophysis; 21, Tibial apophysis from Windsor Tableland. e = embolus, ea = embolic apophysis, c = conductor.



Figures 22–28.—22–23, *Carbinea longiscapa* new species. 22, Expanded palp, prolateral; 23, Embolic region, anterior. 24–28, *Carbinea breviscapa* new species. 24, Feathery hair, leg I; 25, Trichobothrium, tarsal organ on tarsus I; 26, Epigynum; 27, 28, Embolic region male palp; 27, Prolateral view; 28, Embolic apophyses, embolus, conductor, retrolateral view. e = embolus.

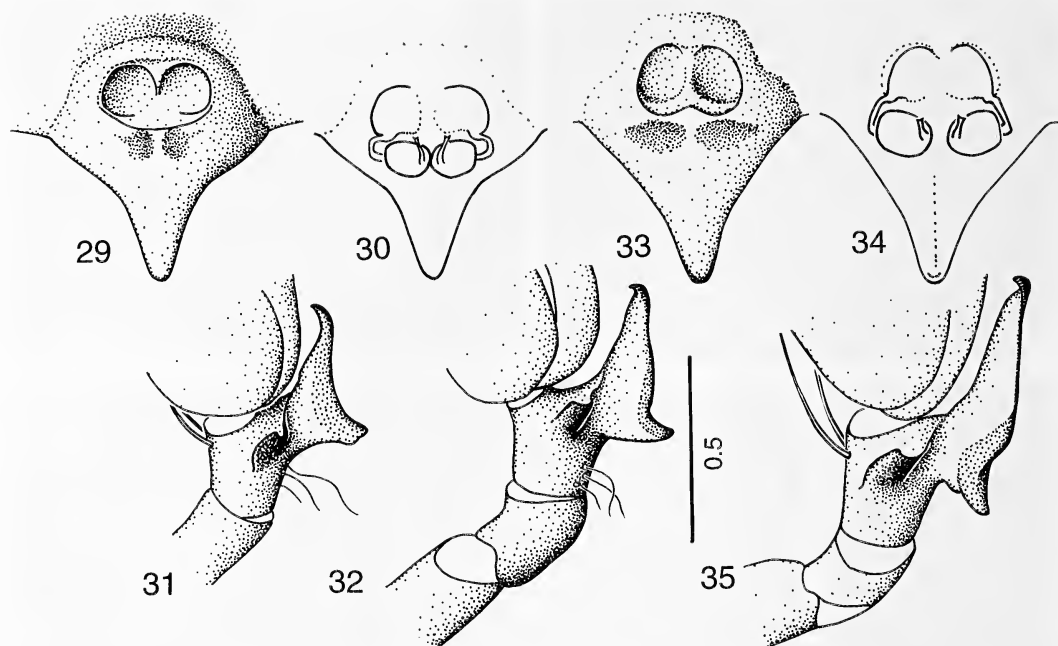
Leichhardt, Mt. Lewis, 16°35', 145°16', 840 m, stick brushing, 18 November 1997, GBM (S39197).

Etymology.—The specific epithet is from the Latin, “longus”, long and “scapus”, stem in reference to the long posterior epigynal scape.

Diagnosis.—Epigynum with very long (0.6–0.7) posterior scape (Figs. 7–10). Tibial

apophysis of male palp more than half the length of the cymbium (Figs. 11–13).

Female: CL 1.8, CW 1.3, AL 2.0, AW 1.3. Straw-colored carapace with two dark longitudinal bands; deep foveal groove. Viewed from the top, eye rows slightly recurved. Ratio of AME:ALE:PME:PLE is 6:11:11:11. Legs 1423 (Table 2) with dark pigmented bands. Notation of leg spines. Femora: I,



Figures 29–35.—*Carbinea* spp. 29–32, *C. wunderlichi* new species. 29–30, Epigynum, ventral, dorsal; 31–32, Tibial apophysis. 31, From Lambs Head; 32, From Mt. Williams. 33–35, *C. robertsi* new species. 33–34, Epigynum, ventral, dorsal; 35, Tibial apophysis.

D110, P011, R001; II, D110, P011, R001; III, D110, P011, R001; IV, D110, P001, R001. Patellae: I, D101; II, D101; III, D101; IV, 001. Tibiae: I, V020; II, V020; III, D001, P101; V111, R011; IV, D001, P111, V111, R101. Metatarsi spined with whorl 4–5 distally. Epigynum with semi-divided fossa; long scape, short insemination ducts to spermathecae. Spinnerets: ALS with two major ampullate spigots, the anterior larger, and about 25 piriform spigots; PMS with a large anterior spigot (minor ampullate) and about 10 other spigots, two of which (cylindrical) have thicker shafts than the rest (aciniforms). PLS with about 25 (aciniform) spigots. Length 3.5–4.0. Females collected from Mossman Bluff (Fig. 10), Pauls Luck and Mt. Demi showed a longer, more attenuated scape.

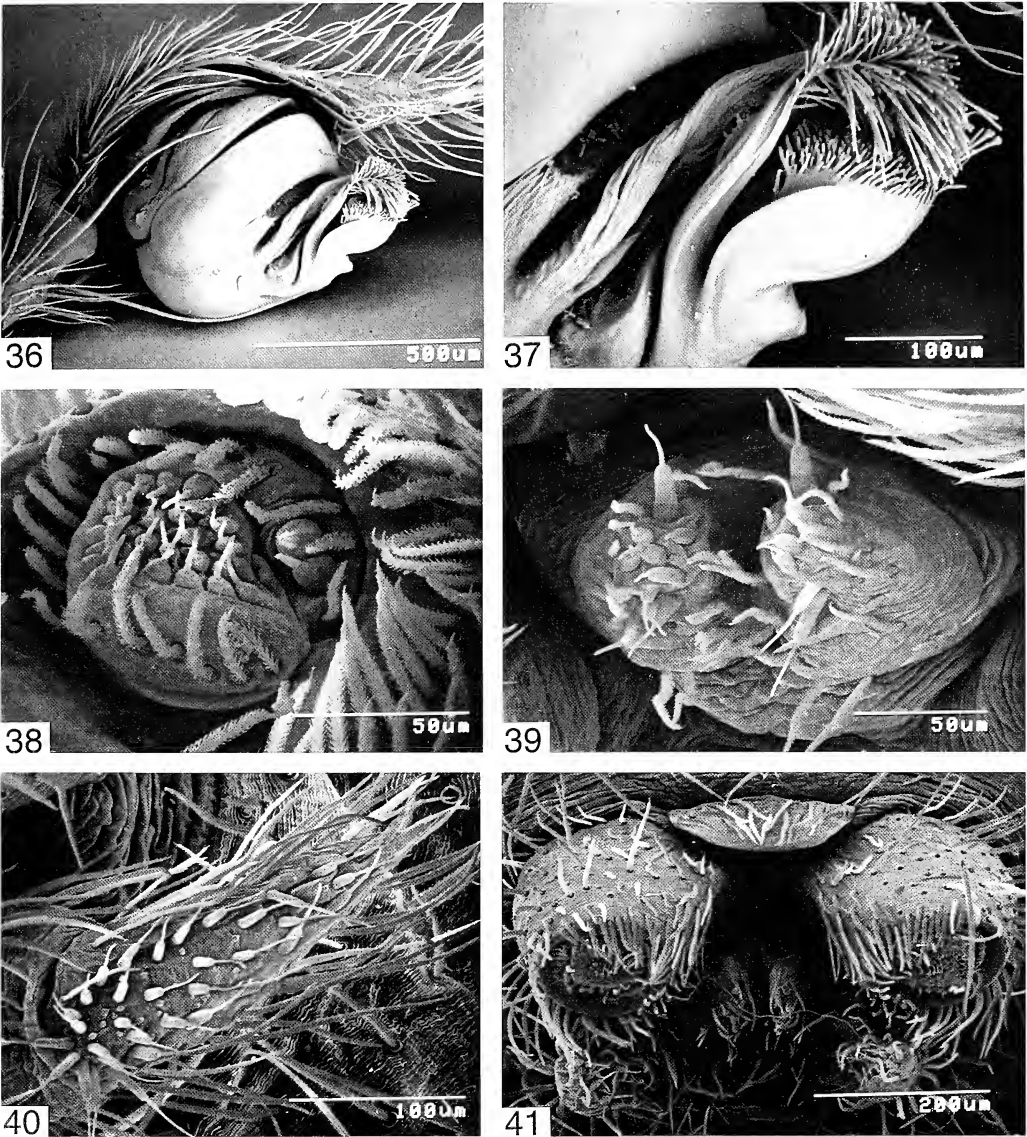
Male: CL 1.8, CW 1.3, AL 1.9, AW 1.3. Coloration and eyes like female. Legs 1423 (Table 2). Notation of spines. Femora: I, D110, P001, R001; II, D110, P011, R011; III, D110, P011, R011; IV, D110, P001, R001. Patellae: I, D001; II, 001; III, 001; IV, 001. Tibiae: I, D100, P011, V221, R011; II, D101, P010, V221, R011; III, D101, P011,

V112, R011; IV, D001, P011, V112, R011. Metatarsi spined with distal whorl 4–5. Palp: short broad tibia; ratio of length to width is 1:0.86. Tegulum with anterior tegular groove. Sperm duct looping over retrolateral tegulum before entering base of embolus. Elaborate embolic apophyses with brushes of plain and “knobbed” setae (Figs. 22–23). RTA more than half as long as cymbium with short blunt retroventral flange. Spinnerets: ALS with one major ampullate spigot and a nubbin. PMS with one large anterior spigot (minor ampullate) and about 10 aciniform spigots; PLS with about 17 aciniform spigots. Length 3.5–4.1.

Distribution.—*Carbinea longiscape* has been collected only on the Carbine Tableland (Fig. 42).

***Carbinea breviscape* new species**
(Figs. 14–21, 24–28, 41–43; Table 4)

Types.—**Australia:** *North Queensland.* Holotype ♀, Stewart Ck., 4 km NNE Mt. Spurgeon, Carbine Tableland, Camp 1, 16°24'S, 145°13'E, 1250–1300 m, PF, 15–20 October 1991, GBM, DC, LR (QM S35235). Paratypes: ♂, 7 km N Mt. Spurgeon,



Figures 36–41.—*Carbinea* spp. 36– 37, *C. wunderlichi* new species from Mt. Williams. 36, Male palp, prolateral; 37, Conductor, base of embolus, embolic apophyses. 38–40, *C. robertsi* new species, female spinnerets. 38, ALS; 39, PMS; 40, PLS. 41, *C. breviscapa* new species, male spinnerets and colulus.

16°22', 145°13', 1200–1250 m, PF, 17–19 October 1991, GBM, DC, LR (S35236); ♀, same data (S35237); ♀, same data as holotype (S35251); ♂, Whypalla State Forest, Windsor Tableland, 16°16', 145°02', 1060 m, PF, summer 1992–3, Scott Burnett (S33163); 2♀, Windsor Tableland, 1.2 km past barracks, 16°15', 145°02', 1060 m, stick brushing, 24 November 1997, GBM (S39201); ♂, Mt. Lewis Rd., 11 km from Hwy. 16°35', 145°17',

1000 m, PF, 18 December 1989–13 January 1990, GBM, GT, ANZSES (S35239); ♀, ♂, Black Mtn., 17 km ESE Julatten, 16°39', 145°29', 1000 m, sieved litter and moss, 29 April 1982, GBM, DY, DC (S35240); ♀, 800–1000 m, PY, 29–30 April 1982 (S35241); ♀, Mt. Formartine South, 10 km N Kuranda 16°43', 145°43', 700 m, PF, 23–24 November 1990, GBM, GT (S35242); ♂, sieved litter (S35243).

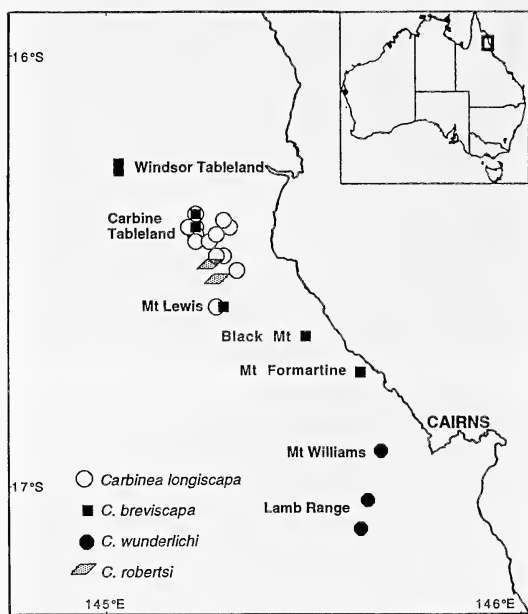


Figure 42.—Map showing distribution of *Carbinea* species.

Etymology.—The specific epithet is from the Latin “brevis”, short and “scapus” stem referring to the very short epigynal scape.

Diagnosis.—Epigynum with short scape (0.3); ♂ tibial apophysis about a quarter the length of the cymbium. Both characters distinguish this species from *C. longiscapa*.

Female: CL 1.8, CW 1.3, AL 2.1, AW 1.6. Coloration and pattern are similar to *C. longiscapa*. Ratio of AME: ALE: PME: PLE is 6:11:11:11. Legs, I, 7.2; II, 5.7; III, 5.3; IV, 7.1. Notation of spines. Femora: I, D110, P001, R001; II, D110, P001, R001; III, D110, P001; IV, D110, P001, R001. Patellae: III, D001; IV, D001. Tibiae: I, V020; II, P001, V020; III, D101, P011, V111, R011; IV, D101, P011, V111, R011. Metatarsi spined with whorl 4–5 distally. Epigynum (Figs. 14, 15, 26). Spinnerets: arrangement of spigots similar to ♀ *C. longiscapa*. Length 3.3–3.9.

Male: (from same locality as ♀, lacking legs II, IV). CL 1.7, CW 1.4, AL 1.8, AW 1.3. Coloration, pattern and eyes are similar to ♀. Legs (Black Mt. specimen) I, 8.1; II, 6.3; III, 5.7; IV, 7.7. Notation of leg spines. Femora: I, D110(I), P00(1)1; II, D110, P011, R011; III, D111, P011, R011; IV, D100. Patellae: I, D001; II, D001; III, D0(1)01; IV, D001. Tibiae: I, D100, P011, V221, R001;

II, D001, P001, V221, R011; III, D101, P011, V111, R011; IV, D101, P011, V012, R011. Metatarsi spined with distal whorl 4–5. Male palp (Figs. 16–18, 27, 28). Tegulum, conductor, embolus, brush-like apophyses and course of sperm duct similar to *C. longiscapa*. RTA about quarter length of cymbium. Spinnerets: arrangement of spigots similar to ♂ *C. longiscapa*. Length 3.1–3.5. Males and females from Black Mountain (Figs. 18, 19), Mt. Formartine and the Windsor Tableland (Fig. 21) are considered to belong in this species.

Distribution.—Most specimens were from the Carbine Tableland (Fig. 42). *Carbinea breviscapa* was also found south of there in the Black Mountain region (Note: not the more northern Black Mountain near Mt. Spurgeon).

Carbinea wunderlich new species
(Figs. 29–32, 36, 37, 42, 43; Table 4)

Types.—**Australia:** *North Queensland.* Holotype ♀, Lambs Head via Mareeba, 17°02'S, 145°38'E, July 1992, J. Wunderlich (QM S35245). Paratypes: ♀, ♂, same data as holotype (S35273); ♂, Lambs Head, 10 km W Edmonton, 1200 m, PF, 10 December 1989–8 January 1990, GBM, JT, HJ (S35244); ♀, Emerald Ck, Lamb Ra, 17°06', 145°37', 950 m, sieved litter, 11 October 1982, GBM, DY, GT (S35246); ♂, Mt. Williams, 16°55', 145°40', 1000 m, sieved litter and moss, 3 December 1993, GBM, HJ (S35234).

Etymology.—The specific name is a patronym in honor of Dr. Jorg Wunderlich who collected the holotype.

Diagnosis.—The epigynal scape is of medium (0.4) length. Tibial apophysis about a third length of cymbium (cf. *C. longiscapa*) with a posterior heel (cf. *C. breviscapa*).

Female: CL 1.7, CW 1.5, AL 2.0, AW 1.6. Coloration, eye measurements, notation of spines similar to *C. longiscapa*. Legs, I, 7.5; II, 5.9; III, 5.3; IV, 7.3. Epigynum (Figs. 29, 30). Length 2.8–3.5.

Male: CL 1.4, CW 1.1, AL 1.4, AW 0.8. Coloration, eyes, notation of spines similar to *C. longiscapa*. Legs, I, 6.8; II, 5.2; III, 4.9; IV, 6.5. Male palp (Figs. 31, 32, 36, 37). Tegulum, conductor and embolus similar to *C.*

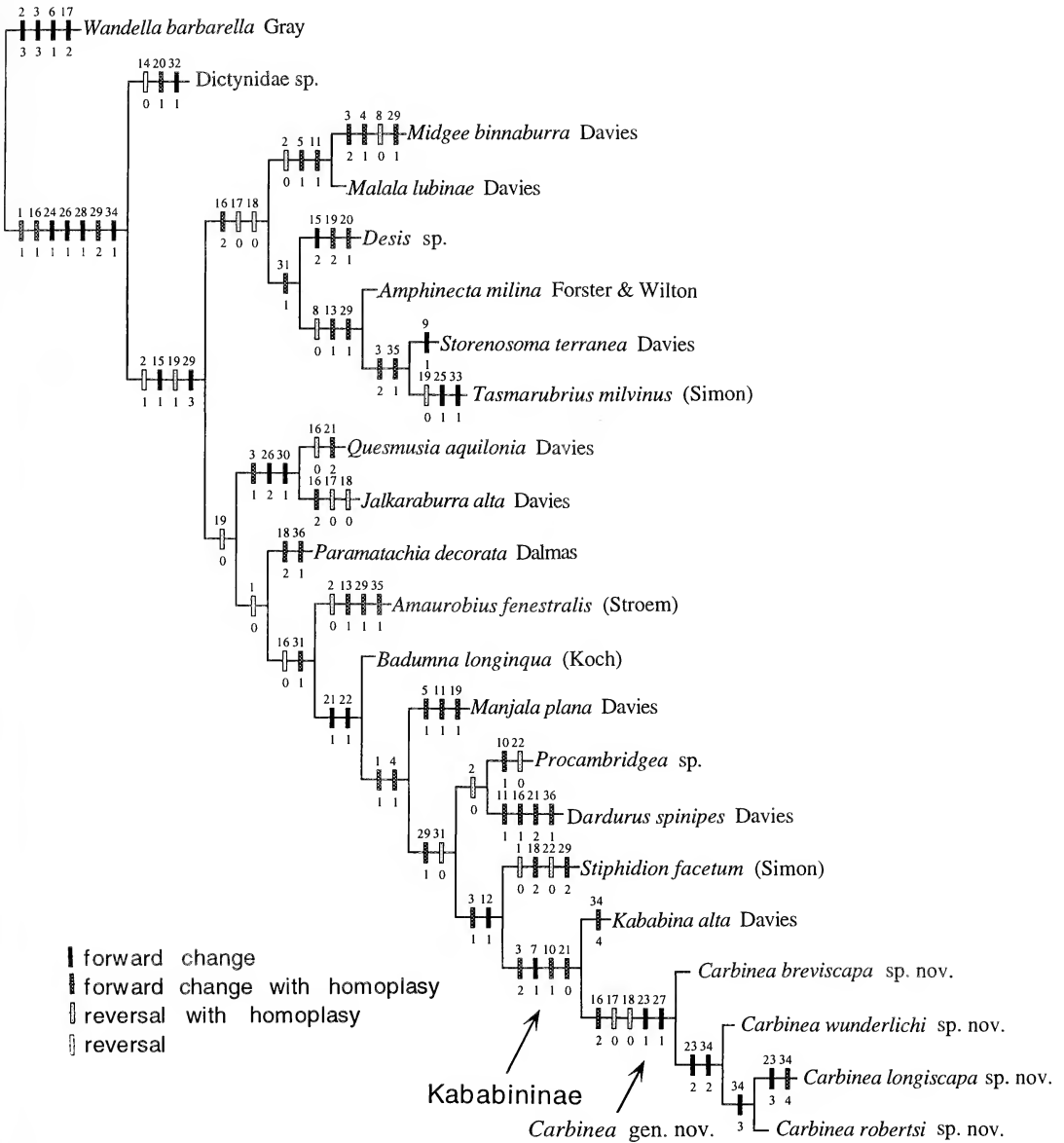


Figure 43.—The single most parsimonious tree showing the cladistic relationships of the Amaurobioidea.

longiscapa. RTA about one-third length of cymbium. Length 2.8–3.5.

Distribution.—From the Lamb Range, SW Cairns (Fig. 42).

Carbinea robertsi new species
 (Figs. 33–35, 38–40, 42, 43; Table 4)

Types.—**Australia:** North Queensland. Holotype ♀, Mt. Lewis, [16°29'S, 145°15'E],

7 November 1975, V.E. Davies (QM S35233). Paratypes: 2♀, ♂, same data as holotype (S35272); ♀, Mt. Lewis Rd. (Hut) 16°31', 146°16', 1200 m, PY trees, 14 July 1996, GBM (39198).

Etymology.—The specific epithet is a patronym in honor of Lewis Roberts, a noted collector from Shiptons Flat, North Queensland.

Diagnosis.—Epigynal scape of medium

Table 3.—Characters and character states, with states in parentheses. Multistate (*) character treated as unordered.

No.	Character
1	AME: as large or larger than ALE (0); smaller than ALE (1)
2	Retromarginal CH teeth: 2+ (0); 2 (1); 1 (2); 0 (3)
3	Promarginal CH teeth: 3+ (0); 3 (1); 2 (2); 0 (3)
4	Long prolateral seta at base of fang: absent (0); present (1)
5	Large frontal CH seta: absent (0); present (1)
6	CH lamina: absent (0); present (1)
7	Foveal area highest: absent (0); present (1)
8	♀ leg I: shorter than leg IV (0); equal to or longer than leg IV (1)
9	Stridulatory ridges on ♂ coxa I: absent (0); present (1)
10	Trochanteral notch: absent (0); present (1)
11	Large ventral spines on tibia and MT I, II: absent (0); present (1)
12	Feathery hairs: absent (0); present (1)
13	MT preening combs: absent (0); present (1)
14	MT TRICH: 2+ (0); 1 (1)
15	Tarsal TRICH: 0 (0); 2+ (1); double row (2)
16	CR: 2 spinning fields (0); 1 spinning field (1); absent (2)
17	CR spigots: absent (0); longitudinally ribbed (1); annulate (2)
18	Calamistrum: absent (0); proximal (1); proximo-medial (2)
19	MAP ♀ ALS: 2 (0); 1 and nubbin (1); 1 (2)
20	Position of MAP ♀ ALS: mesal (0); anterior (1)
21*	PCR ♀ PMS: one shaft per base (0); more than one shaft (1); absent (2)
22	Medial EPIG fossa: absent (0); present (1)
23	Posterior EPIG scape: absent (0); short (1); medium (2); long (3)
24	Insemination duct: absent (0); present (1)
25	EPIG lateral projections: absent (0); present (1)
26	E direction: straight (0); clockwise (1); anticlockwise (2)
27	Proximal E APOPH: absent (0); present (1)
28	Parembolic process: present (0); absent (1)
29*	Conductor: absent (0); rounded (1); large T-shaped (2); s-shaped-falciform (3)
30	Secondary conductor: absent (0); present (1)
31	Median APOPH: absent (0); present (1)
32	Orientation of CB to bulb: dorsal (0); mesal (1)
33	Paracymbium: absent (0); present (1)

Table 3.—Continued.

No.	Character
34	RTA to CB length: absent (0); quarter or less (1); third (2); half (3); more than half (4)
35	Dorsal branch of RTA: absent (0); present (1)
36	Palpal patellar APOPH: absent (0); present (1)

(0.4) length (cf. *C. longiscapa*). Tibial apophysis long (cf. *C. breviscapa* and *C. wunderlichi*).

Female: CL 1.9, CW 1.4, AL 2.1, AW 1.4. Coloration, eye measurements, notation of spines similar to *C. longiscapa*. Legs, I, 7.5; II, 5.8; III, 5.4; IV, 7.3. Epigynum (Figs. 33, 34). Spinnerets (Figs. 38–40): ALS with two major ampullate spigots and about 25 piri-form spigots. PMS with a large anterior spigot (minor ampullate) and about 10 smaller spigots, 2–3 with thicker shafts from cylindrical glands, the others from aciniform glands. PLS with about 25 aciniform spigots. Length 3.6–4.0.

Male: CL 1.7, CW 1.3, AL 1.8, AW 1.2. Legs, I, 7.9; II, 6.1; III, 5.6; IV, 7.5. Tegulum, conductor, embolus similar to *C. longiscapa*. RTA long, half length of cymbium (Fig. 35).

Distribution.—*Carbinea robertsi* was found at one site on Mt. Lewis (Fig. 42).

RELATIONSHIPS OF CARBINEA

A cladistic analysis examined 36 characters (Table 3) for relationships of *Carbinea* spp. and 18 other taxa (names and authors given on cladogram, Fig. 43). Voucher specimens of the taxa are deposited in the QM. Outgroup comparison was with the Australian spiders *Wandella barbarella*, a filistatid and an undescribed dictynid. A data matrix (Table 4) was assembled in MacClade 3.01 (Maddison & Maddison 1992). Unknown characters are represented by “?”, inapplicable characters by “-”. The data were analyzed in PAUP version 3.1.1 (Swofford 1993) and replicated in Hennig. A heuristic search of the data with 10 random-addition sequences and TBR branch swapping generated one most parsimonious tree (Fig. 43); length 103, CI = 0.52, CI excluding uninformative characters = 0.48, RI = 0.67, RC = 0.35. Char-

Table 4.—Data matrix

		10	20	30
<i>Wandella</i>	033001010	0000100212	00--000000	0000000
Dictynidae A	120000010	0000001112	1000101012	0010100
<i>Badumna</i>	010000010	0000110110	0110101013	0100100
<i>Paramatachia</i>	010000010	0000111120	0000101013	0000101
<i>Desis</i>	110000010	0000122002	1-00101013	0100100
<i>Quemusia</i>	111000010	0000110110	0200102013	1000100
<i>Jalkaraburra</i>	111000010	0000112000	0-00102013	1000100
<i>Amphinecta</i>	110000000	000111200?	0-00101011	0100100
<i>Amaurobius</i>	000000010	0001110110	0000101011	0100110
<i>Storenosoma</i>	112000001	0001112001	0-00101011	0100110
<i>Tasmarubrius</i>	112000000	0001112000	0-00111011	0101110
<i>Procambidgea</i>	100100010	1000110110	0100101011	0000100
<i>Stiphidion</i>	011100010	0010110120	0100101012	0000100
<i>Midgee</i>	102110000	0100112001	0-00101011	0000100
<i>Dardurus</i>	100100010	0100111110	0210101011	0000101
<i>Manjala</i>	110110010	0100110111	0?10101013	0100100
<i>Malala</i>	100010010	0100112001	0-00101013	0000100
<i>Kababina</i>	112100110	1010110110	0010101011	0000400
<i>Carbinea longiscapa</i>	112100110	1010112000	0-13101111	0000400
<i>C. breviscapa</i>	112100110	1010112000	0-11101111	0000100
<i>C. wunderlichi</i>	112100110	1010112000	0-12101111	0000200
<i>C. robertsi</i>	112100110	1010112000	0-12101111	0000300

acters were mapped in CLADOS version 1.2 (Nixon 1992) with DELTRAN optimization.

Conclusions.—*Wandella* and Dictynidae A appear as distinct from the ingroup which is regarded as the superfamily Amaurobioidea. This is composed of two clades, the first of which includes *Desis* (Desidae), *Amphinecta* (Amphinectidae) and *Tasmarubrius* (Davies 1998). The second clade includes *Amaurobius* (Amaurobiidae), *Stiphidion* (Stiphidiidae) and the metaltellines *Quemusia* and *Jalkaraburra*. *Kababina* and *Carbinea* are the only genera in this clade that form a well-supported monophyletic group Kababininae, which was previously (Davies 1995) placed in the Amphinectidae and from which it is now withdrawn. The group appears closest to *Stiphidion*; however, separation of the Kababininae would render the base of the clade paraphyletic. Until further description and analysis of the basal members of this clade are extended, the family placements of the clade will remain problematic.

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SPIDERS OF THE GENUS *HEPTATHELA* (ARANEAE, LIPHISTIIDAE) FROM VIETNAM, WITH NOTES ON THEIR NATURAL HISTORY

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ABSTRACT. Spiders of the family Liphistiidae collected from northern Vietnam are taxonomically studied. Two new species of the genus *Heptathela* are described under the names, *H. abca* (from Yen Bai) and *H. cucphuongensis* (from Cuc Phuong National Park). Some natural history and zoogeographic notes of the new species are given.

About 90 years ago, a liphistiid spider was recorded from Kha-lé in the area of the river Song Luc Nam northeast of Hanoi (Simon 1908). This spider was erroneously identified as *Liphistius birmanicus* Thorell 1897, originally described from Burma. Because this record was based on a misidentification, Bristowe (1933) gave a new name *Liphistius tonkinensis* for the same spider. Although the genus *Heptathela* was already known at that time (Kishida 1923), the Vietnamese species was misplaced in *Liphistius* for a long time. Haupt (1983) finally redescribed the species and transferred it to *Heptathela*. *Heptathela tonkinensis* was the first heptatheline recorded.

In 1995 and 1997, I had opportunities to participate in entomological expeditions to northern Vietnam, made by the National Science Museum, Tokyo. Although it was hard to find preserved forests in the country, researchers on our expeditions collected many spider specimens, including those of *Heptathela*. *Heptathela tomokunii*, the second species of the genus from Vietnam, was described from Mt. Tam Dao, about 60 km northwest of Hanoi, based on this material (Ono 1997a).

The present paper deals with the results of a taxonomic study of liphistiids obtained during the second Vietnam expedition in 1997. Two further new species of the genus *Heptathela* are described from Yen Bai and Cuc Phuong National Park. Some biological data of these spiders are noted.

METHODS

Between 26 September–25 October 1997, liphistiid spiders were collected at Yen Bai

(elevation 120 m), and in the National Park of Cuc Phuong (350 m) in northern Vietnam (Fig. 1). Some biological observations (for example, the shape of egg sac and the diameter of trapdoor) were made in the field. The spiders were kept in 75% alcohol and taxonomically studied in laboratory of the museum at Tokyo. After morphological observations, two new species were recognized.

The type specimens of the new species are deposited in the collection of the Department of Zoology, National Science Museum, Tokyo (NSMT). The abbreviations herein used are as follows: ALE, anterior lateral eye; AME, anterior median eye; PLE, posterior lateral eye; PME, posterior median eye. Morphology of genital organs chiefly follows Haupt (1979).

DESCRIPTIONS OF NEW SPECIES

Heptathela abca new species (Figs. 2–4, 14)

Diagnosis.—This new species seems to be related to *Heptathela tomokunii* Ono 1997, described from Mt. Tam Dao, Vinh Phu Province, Vietnam, having the same construction of female genitalia. However, the new species can be distinguished from the latter by the shape of spermathecae (receptaculula seminis): main, lateral bursae of *Heptathela abca* are reniform and are set on their bases, while those of *H. tomokunii* are oval and close to the lamellar interior part of the genitalia; the tubular stems of median bursae of *H. abca* are much longer than those of *H. tomokunii* (cf. Fig. 3 of this paper and fig. 6 in Ono 1997a).

Etymology.—The specific epithet is an arbitrary combination of letters.

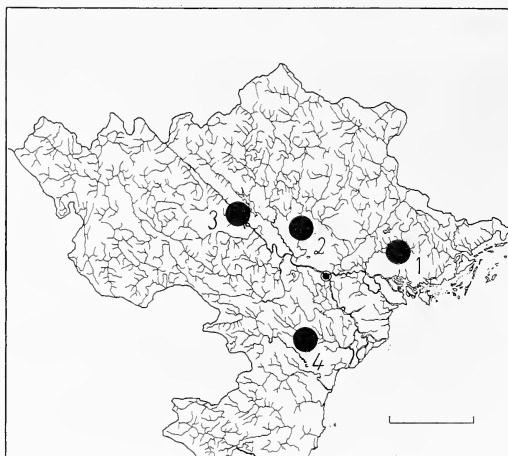


Figure 1.—Records of the spiders of the genus *Heptathela* in Vietnam. 1. Song Luc Nam, Ha Bac Province, *Heptathela tonkinensis* (Bristowe 1933); 2. Tam Dao, Vinh Phu Province, *Heptathela tomokunii* Ono 1997; 3. Yen Bai, Yen Bai Province, *Heptathela abca* new species; 4. Cuc Phuong, Ninh Binh Province, *Heptathela cucphuongensis* new species. [Small circle = Hanoi; upper line of the frame, 24°N, bottom, 19°N, left, 102°E, right, 108°E; scale = 100 km]

Type series.—Female holotype, VIETNAM, Yen Bai Province, Yen Bai (elevation 120 m), 13 October 1997, H. Ono leg. (NSMT-Ar 3830); paratypes: 2♀, same data as for holotype (NSMT-Ar 3831-3832), 3♀ and 2 juveniles, same locality and collector as for holotype, 14 October 1997 (NSMT-Ar 3833-3837).

Description.—Female (male specimen not available). Measurements based on holotype: body length 17.5 mm; prosoma length 8.4 mm, width 7.1 mm; opisthosoma length 9.1 mm, width 6.8 mm; lengths of palp and legs [total length (femur + patella + tibia + metatarsus + tarsus)]: palp 15.3 mm (5.3 + 2.7 + 3.4 + – + 3.9); leg I 17.8 mm (5.8 + 3.0 + 3.5 + 3.5 + 2.0); II 18.2 mm (5.8 + 2.9 + 3.4 + 3.9 + 2.2); III 19.9 mm (5.7 + 3.3 + 3.4 + 4.7 + 2.8); IV 29.0 mm (8.0 + 3.7 + 5.1 + 8.2 + 4.0). Variation of body length: 12.1–20.2 mm. Head high; ocular tubercle wider than long, ALE > PLE > PME > AME (9.6:8.3:4.6:1 in ratio), AME small, clypeus wider than ALE-ALE, median ocular area trapezoidal, wider than long. Chelicera with 11 teeth (3 large and 8 small) on promargin of fang furrow. Leg formula IV, III, II, I; su-

perior claws of tarsi each with 2 teeth; claw of palp without tooth. Opisthosoma ovate, longer than wide; posterior median spinnerets reduced, completely fused, with setae (Fig. 4). Two pairs of spermathecae present (Fig. 2–3); main, lateral bursae set on thick bases, reniform, with many middle-sized, granulate tubercles; median ones small, on long tubular stems.

Coloration.—Prosoma brown, cephalic part not darker, ocular tubercle black; chelicerae brown, basally lighter, fang and fang furrow reddish-brown, sternum and coxae of legs and palps light reddish-brown, other segments of legs and palps brown. Opisthosoma grayish-brown, dorsal sclerites blackish-brown, ventral sclerites and spinnerets yellowish-brown.

Remarks.—A female specimen (NSMT-Ar 3839) collected at a village about 15 km northwest of Yen Bai on 6 October 1997 by myself tentatively identified as *Heptathela abca*. However, the shape of female genitalia of the spider (Figs. 5–6) is slightly different from that of holotype.

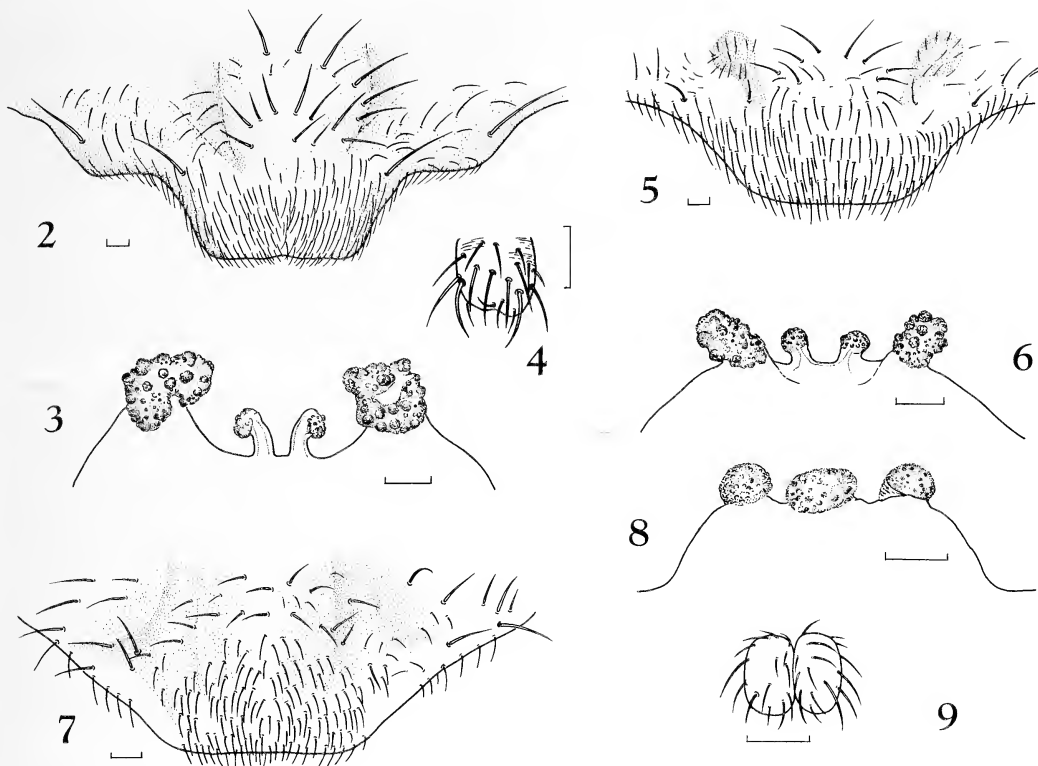
Heptathela cucphuongensis new species
(Figs. 7–9, 17)

Diagnosis.—This new species is close to *Heptathela hunanensis* Song & Haupt 1984, described from Qianyang County, Hunan Province of China. In both the species, median spermathecae are fused and form a large bursa. However, the new species is distinguishable from the Chinese spider by the shape of lateral bursae without bases (*cf.* Fig. 8 of this paper and fig. 3e in Song & Haupt 1984).

Etymology.—The specific epithet is derived from the type locality.

Type series.—Female holotype, VIETNAM, Ninh Binh Province, Gia Vien, Cuc Phuong (elevation 350 m), 30 September 1997, H. Ono leg. (NSMT-Ar 3822); paratypes: 2♀ and 7 juveniles, same data as for holotype (NSMT-Ar 3823-3827).

Description.—Female (male specimen not available). Measurements based on holotype: body length 17.5 mm; prosoma length 7.8 mm, width 6.1 mm; opisthosoma length 8.1 mm, width 5.4 mm; lengths of palp and legs [total length (femur + patella + tibia + metatarsus + tarsus)]: palp 12.2 mm (4.4 + 2.3 + 2.5 + – + 3.0); leg I 15.5 mm (5.3 + 2.5 + 3.1 + 2.9 + 1.7); II 15.7 mm (5.2 + 2.7 + 2.8 + 3.3 + 1.7); III 16.6 mm (5.1 + 2.7 +



Figures 2–9.—2–4, *Heptathela abca* new species, female holotype, NSMT-Ar 3830; 5–6, *Heptathela* sp. (?*H. abca*) from 15 km NW of Yen Bai; 7–9, *Heptathela cucphuongensis* new species, female holotype, NSMT-Ar 3822. 2, 5, 7. Genital area, ventral view; 3, 6, 8. Spermathecae, dorsal view; 4, 9. Posterior median spinnerets, ventral view. [Scales = 0.25 mm]

2.9 + 3.8 + 2.1); IV 23.4 mm (6.8 + 3.2 + 4.2 + 6.4 + 2.8). Variation of body length: females 15.1–17.5 mm. Head high; ocular tubercle slightly longer than wide, ALE > PLE > PME > AME (8 : 7.6 : 4.3 : 1 in ratio), clypeus wider than ALE-ALE, median ocular area trapezoidal, slightly wider than long. Chelicera with 12 (right) or 13 (left) teeth (3 large and 9 or 10 small) on promargin of fang furrow. Leg formula IV, III, II, I; superior claws of tarsi I with 3 teeth, II–IV each with 2 teeth; claw of palp without tooth. Opisthosoma ovate, longer than wide; posterior median spinnerets not fused (Fig. 9). Three spermathecae present (Figs. 7–8); lateral bursae without bases, globular, with many small granulate tubercles; median one unpaired, oval, granulate, without stem.

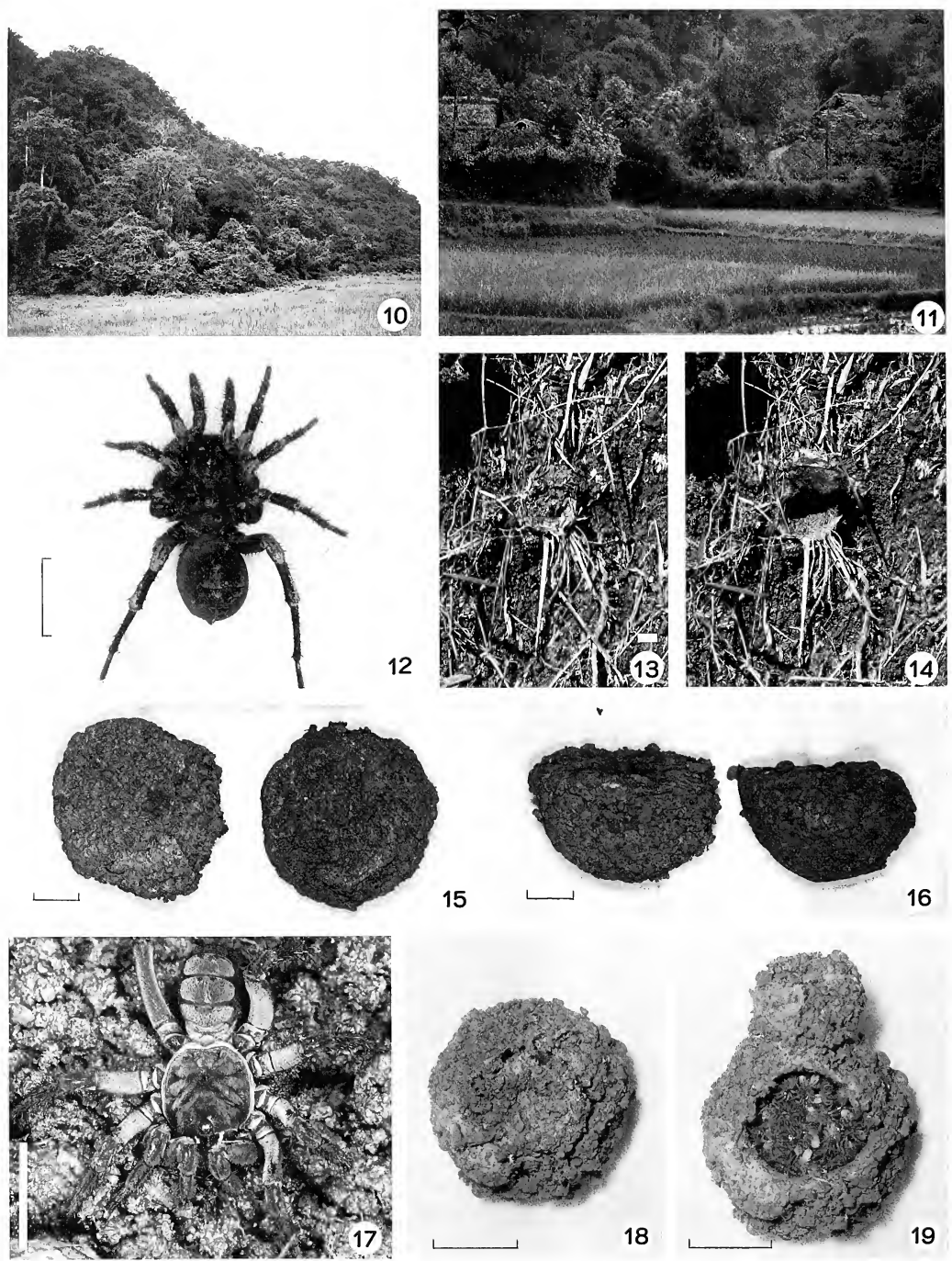
Coloration: Prosoma blackish-brown, cephalic part darker, ocular tubercle black; chelicerae blackish-brown, basally light yellowish-brown, fang and fang furrow reddish-brown, sternum and coxae of legs and palps grayish-

brown, other segments of legs and palps dark gray, femora much darker. Opisthosoma dark gray, dorsal sclerites blackish-brown, ventral sclerites and spinnerets yellowish-brown. Color in life bluish-black.

NATURAL HISTORY NOTES

As an agricultural country in Asia, Vietnam has developed at the expense of deforestation for centuries. Sub-tropical and tropical lowlands are totally cultivated mainly for rice production. On the other hand, the people of various tribes farm with primitive methods on temperate highlands, and cut trees for firewood. Thus, primary forests, the habitat of liphistiid spiders, are only found scattered on the mountainous hinterland. Tam Dao (1230 m elevation at peak) is one of the typical areas preserved by the country. Spiders of *Heptathela tomokunii* live there (Ono 1997a).

In Cuc Phuong National Park, evergreen broad-leaved forests and occasional damp bushes are preserved in nature (Fig. 10). Spi-



Figures 10–19.—10. Habitat of *Heptathela cucphuongensis* new species at Cuc Phuong; 11. Habitat of *Heptathela abca* new species at Yen Bai; 12. Holotype female of *Heptathela abca* new species; 13–14. A retreat with grass-blades of *Heptathela abca* new species; 15–16. Egg sacs of *Heptathela abca* new species; 17. Holotype female of *Heptathela cucphuongensis*; 18–19. Egg sac of *Heptathela cucphuongensis* new species. [Scales = 10 mm]

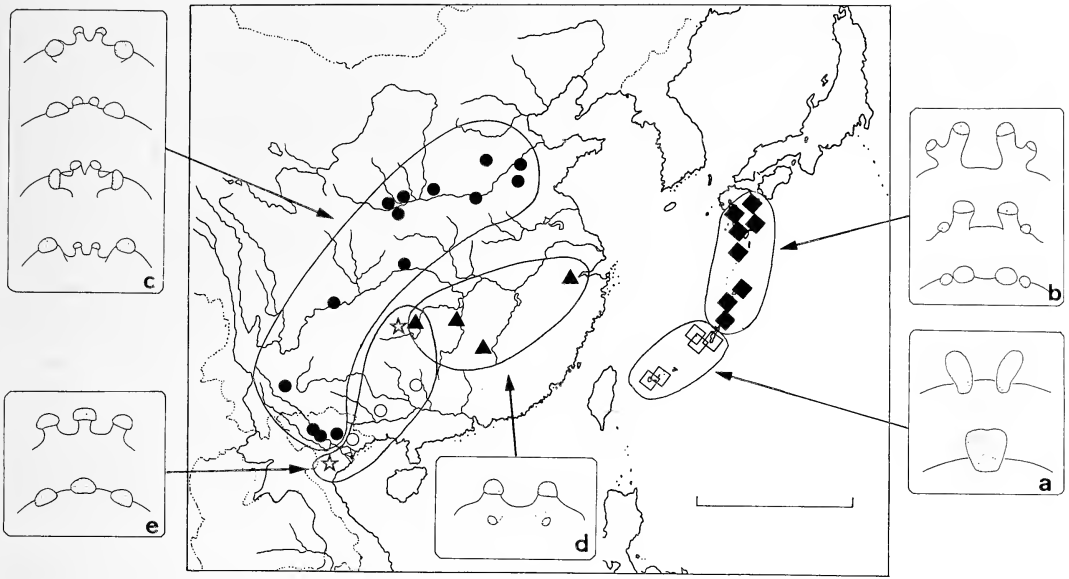


Figure 20.—Distribution of the species of the subfamily Heptathelinae in East Asia: The symbols correspond to the groups A-E in the text: □ = Group A, ■ = Group B, ● = Group C, ▲ = Group D, and ☆ = Group E. The open circles (○) indicate species whose female is unknown. a-e are diagrams of female genitalia. [Scale = 1000 km]

ders of *Heptathela cucphuongensis* were found along roadsides at the forest edge. They built retreats in the soil about 15–25 cm deep, as is typical of the genus *Heptathela*. The trapdoor of the holotype female was the largest at 35 mm wide and 27 mm long. Globular egg sacs made with soil and 24–27 mm in diameter (Fig. 18) were found at the bottom of the tubular retreats, with 120 spiderlings closely packed in the sac (Fig. 19).

As an unusual case, *Heptathela abca* was found in a village near the city of Yen Bai. The environmental difference between that village and other cultivated areas on lowlands, in which no liphistiids were found, is the existence of trees left around the houses and rice fields (Fig. 11). The earth was kept moist. The openings of some retreats were decorated with fragments of grass (Figs. 13–14). The trapdoors of the spiders were measured: 43 × 33, 33 × 29, 30 × 26, 28 × 25, 24 × 21 and 17 × 15 mm. Egg sacs were semiglobular and about 35 mm in diameter (Figs. 15–16). Respectively, 201 and 221 spiderlings emerged from the sacs in November.

ZOOGEOGRAPHIC NOTES

Trapdoor spiders of the family Liphistiidae (Araneae, Mesothelae) are composed of two

recent subfamilies, Liphistiinae and Heptathelinae, both distributed in East Asia. More than 40 species of the single genus *Liphistius* Schödte 1849 were described under the former subfamily from Myanmar (Burma), Thailand, the Malay Peninsula and Sumatra (newest informations: Schwendinger 1996; Platnick, Schwendinger & Steiner 1997), while 29 species of two genera, *Heptathela* Kishida 1923 and *Ryuthela* Haupt 1983 were known in the latter subfamily in Japan, China and Vietnam (Haupt 1983; Song & Haupt 1984; Ono 1996, 1997a & b, 1998 and this paper).

Based on characteristics of the female genitalia (males are unknown in many species), the heptatheline species are classified into five groups as follows, which are grouped in an allopatric arrangement (Fig. 20). Their phylogenetic relationships are not considered in this paper. Vietnamese species belong to two different groups.

Group A.—*Ryuthela nishihirai* Haupt 1979, *R. ishigakiensis* Haupt 1983, *R. owadai* Ono 1997, *R. sasakii* Ono 1997, *R. secundaria* Ono 1997, and *R. tanikawai* Ono 1997. A pair of monolobal spermathecae present, both the spermathecae close to each other, or fused

with one large opening (Fig. 20a). Distribution: Japan (southern part of the Ryukyu Islands). [Although the genus *Ryuthela* was synonymized with *Heptathela* by Raven (1985), I follow the contrary treatment by Haupt (1990).]

Group B.—*Heptathela kimurai* (Kishida 1920), *H. amamiensis* Haupt 1983, *H. higoensis* Haupt 1983, *H. kanenoi* Ono 1996, *H. kikuyai* Ono 1998, *H. nishikawai* Ono 1998, *H. yaginumai* Ono 1998, *H. yakushimaensis* Ono 1998, *H. yanbaruensis* Haupt 1983. A pair of spermathecae present, spermathecae bilobal with secondary process laterally (Fig. 20b). Distribution: Japan (Kyushu and the northern part of the Ryukyu Islands).

Group C.—*Heptathela sinensis* Bishop & Crosby 1932, *H. bristowei* Gertsch 1967, *H. jiangnanensis* Chen *et al.* 1988, *H. schensiensis* (Schenkel 1953), *H. heyangensis* (Zhu & Wang 1984), *H. yunnanensis* Song & Haupt 1984, *H. tomokunii* Ono 1997 and *H. abca* new species. Two pair of spermathecae present, the lateral bursae larger and usually on thick bases, the median ones small and on tubular stems (Fig. 20c). Distribution: China (from Hebei to Yunnan) and Vietnam.

Group D.—*Heptathela hangzhouensis* Chen, Zhang & Zhu 1981 and *H. cipingensis* (Wang 1989). Two pair of spermathecae present, the main bursae situated in more median position, the median ones moved posteriorly and situated at the base of main bursae (Fig. 20d). Distribution: China (from Zhejiang to Hunan).

Group E.—*Heptathela hunanensis* Song & Haupt 1984 and *H. cucphuongensis* Ono new species. Three spermathecae present, two lateral bursae and one median one in same size (Fig. 20e). Distribution: China (Hunan) and Vietnam.

Female unknown.—*Heptathela tonkinensis* (Bristowe 1933) and *H. hongkong* Song & Wu 1997.

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ON THE PHYLOGENETIC RELATIONSHIPS OF *SISICOTTUS HIBERNUS* (ARANEAE, LINYPHIIDAE, ERIGONINAE)

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ABSTRACT. *Carorita hiberna* NEW COMBINATION, a species with many putative autapomorphies known from one sex and few specimens, is transferred from *Sisicottus*. This transfer is based on a modified version of a cladistic analysis of erigonine relationships by G. Hormiga which incorporated 43 spider taxa scored for 73 characters. The modified analysis features 46 taxa scored for 74 characters. The resulting cladogram placed *C. hiberna* sister to *C. limnaea*, the type species of *Carorita*. It is concluded that *C. hiberna* is better placed in *Carorita* than in either a new monotypic genus or in *Sisicottus*. *Carorita hiberna* is redescribed and the monophyly of *Carorita* as currently circumscribed is discussed.

Carorita hiberna (Barrows 1945) NEW COMBINATION (Linyphiidae, Erigoninae) was inexplicably described as a member of the genus *Sisicottus* Bishop & Crosby 1938. *Carorita hiberna* is a very unusual erigonine species that shares none of the synapomorphies that unite *Sisicottus* (Zujko-Miller 1999). *Carorita hiberna* is known only from three male specimens from the Great Smoky Mountains National Park, North Carolina, USA. After revising *Sisicottus* (Zujko-Miller 1999), I was left with three alternatives as to the fate of *C. hiberna*: I could keep it in *Sisicottus*, which would leave *Sisicottus* polyphyletic; I could erect a new monotypic genus for it; or I could transfer it to the genus which contains its closest relatives. *Carorita hiberna* features many apparently apomorphic character states in the form of the male palpus, and it was not obvious to me what genus contained its closest relatives. I chose to seek the closest relatives of *C. hiberna* using phylogenetic methods. By placing *C. hiberna* in a phylogenetic context, I was able to formulate a testable phylogenetic hypothesis. My cladistic analysis identified *Carorita limnaea* (Crosby & Bishop 1927), the type species of *Carorita* Duffey & Merrett 1963, as the sister taxon of *C. hiberna*. With the transfer of *C. hibernus*, *Carorita* currently contains three species.

METHODS

I cleared specimens in methyl salicylate (Holm 1979) and positioned them for illustra-

tion using a temporary slide mount (Coddington 1983). I made sketches using a camera lucida fitted to a Leica DMRM compound microscope at 400 \times . Further observations were made using a Leica MZ APO dissecting microscope. Museum acronyms for specimen depositories appear in the acknowledgments.

CLADISTIC ANALYSIS

The cladistic analysis by Hormiga (in press) is the most rigorous hypothesis of erigonine relationships to date and is the logical starting point for questions of relationships within the Erigoninae. The original analysis incorporates 43 terminal taxa, including 31 erigonine genera, scored for 73 characters. My modified version of Hormiga's analysis incorporates three additional taxa, one new character, and one recoded character.

Carorita hiberna, *C. limnaea*, and *Sisicottus montanus* (Emerton 1882) were added to Hormiga's (in press) matrix. *Carorita limnaea* was included because it appears to share some potentially synapomorphic character states with *C. hiberna* including a looped sperm duct in the tegulum, a tuberculate radical tailpiece, and a suprattegulum separated from the tegulum by a membranous region so that it appears to form a distinct sclerite. *Sisicottus* was included to test the implicit phylogenetic hypothesis of Barrows (1945) that *C. hiberna* plus *Sisicottus* form a monophyletic group.

Several character states remain unknown for *C. hiberna* because females are unknown and males are rare and not available for irreversible methods of examination. The male cephalothorax was not examined using scanning electron microscopy to search for cuticular pores in the clypeal region (character 50) or to examine details of the stridulatory striae on the chelicerae (character 56). No abdomens were digested for examination of the tracheal system (characters 51, 52). *Carorita hiberna* was coded as follows: 0001310110 1210110101 1201000101 3????????? 000000000? ?001?0?1 00011?0?1 1??1

Carorita limnaea was coded as follows: 0001310110 1210110101 1501000101 300-000100 0000000000 0-00120111 0011100101 1??1. *Carorita limnaea* was given a unique character state for the shape of the radical tail piece (character 22). In *C. limnaea*, the tailpiece extends both dorsally and ventrally from its origin distal to the origin of the embolus. Coding of *C. limnaea* was based on examination of the following specimens: **UNITED STATES: Maine:** Piscataquis County, 2.3 km ESE of Soubunge Mtn., dense spruce-fir forest, Line I, Stn. 1, T4 R11, WELS, 1 June 1978, pitfall collection, 1♂, (D.T. Jennings, M.W. Houseweart, USNM); **New York:** McLean, mud pond, 42°32'N, 76°18'W, 30 May 1921, 8♂17♀, (C.R. Crosby, AMNH).

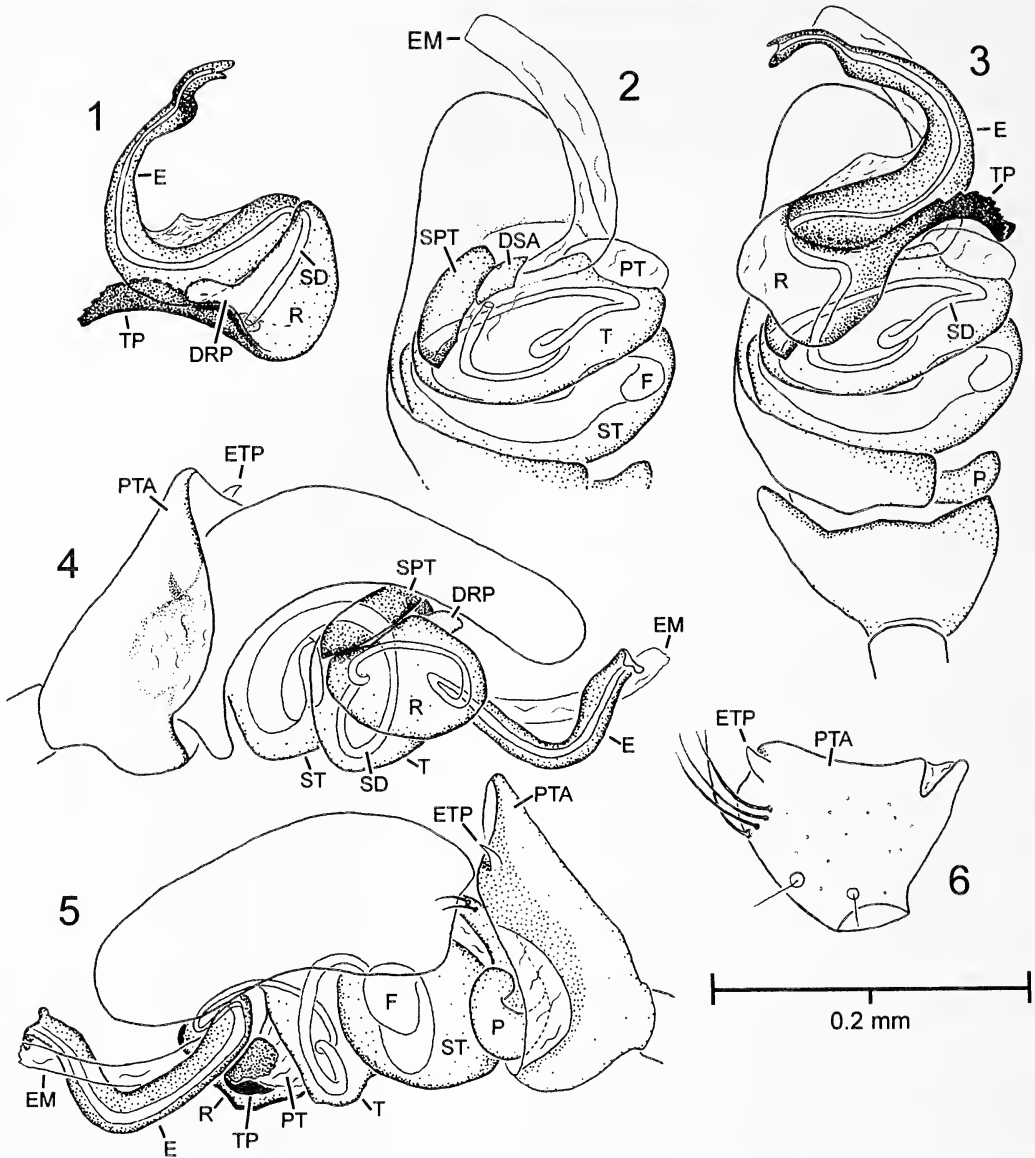
Sisicottus montanus was coded as in Zujko-Miller (1999). Character 74 was scored with a zero. Coding of *S. montanus* was based on examination of the following specimens: **UNITED STATES: Massachusetts:** Berkshire County, Mt. Greylock, 3400 feet, deciduous litter, 15 October 1990, 2♂1♀, (R.L. Edwards, USNM).

Hormiga's (in press) analysis was modified by the addition of one new character and the recoding of an existing character. Both characters pertain to structures that are synapomorphies of the Linyphiidae (the suprategulum and the linyphiid radix) so character states for linyphiid taxa other than *C. limnaea*, *C. hiberna*, and *S. montanus* were determined using Hormiga (1994, in press). Character 74 is the texture of the radical tailpiece which is tuberculate in *C. limnaea* and *C. hiberna*. In all other taxa with a radical tailpiece, this sclerite is more or less smooth. Taxa without a radical tailpiece were coded as inapplicable

for this character. The junction between the tegulum and the suprategulum (character 12) was recoded. Character 12 documents the membranous hinge between the tegulum and the suprategulum in *Stemonyphantes* Menge 1886 (van Helsdingen 1968; Hormiga 1994). In the context of Hormiga's analysis, this character state is autapomorphic and character 12 is not phylogenetically informative. I have added a third state to character 12 and it is now coded as follows: Suprategulum: 0 = continuous with tegulum; 1 = articulated; 2 = separate from tegulum (Figs. 7, 9). In *Carorita limnaea*, *C. hiberna*, *Asthenargus paganus* (Simon 1884), *Gongyliellum vivum* (O. Pickard-Cambridge 1875) and *Erigone psychrophila* Thorell 1871, there is a membranous division between the sclerotized parts of the tegulum and the suprategulum so that the suprategulum appears to be a distinct sclerite rather than a more heavily sclerotized distal portion of the tegulum. This is the new character state coded as 2. In most other linyphiids, the tegulum and the suprategulum are joined by a region of continuous sclerotization and only part of the junction between the tegulum and the suprategulum is membranous. In *Stemonyphantes*, the junction between the tegulum and the suprategulum is a wide flexible hinge (Hormiga 1994, fig. 2c). Also, the tegular-suprategular junction is unusual in *Stemonyphantes* because it is on the ventral face rather than the mesal face of the palpal bulb.

Analysis.—I used PAUP version 3.1 (Swofford 1993), Hennig86 version 1.5 (Farris 1988) and NONA version 1.6 (Goloboff 1993) to search the data (46 taxa, 74 characters) for the most parsimonious topology. In PAUP, I ran a heuristic search with 100 replicates of random taxon addition subjected to tree bisection-reconnection branch swapping. In Hennig86, I used the "mh*,bb*" search strategy. In NONA, I ran a search under the "amb=" setting (modified rule 3; see Codrington & Scharff 1994; Zujko-Miller 1999) with the "mult*" random taxon addition algorithm for 100 replicates followed by the "max*" branch-swapping algorithm. I used MacClade (Maddison & Maddison 1992) to analyze character optimization.

Successive character weighting (Farris 1969; Carpenter 1988) by the maximum value of the rescaled consistency index was performed in PAUP with the base weight set to

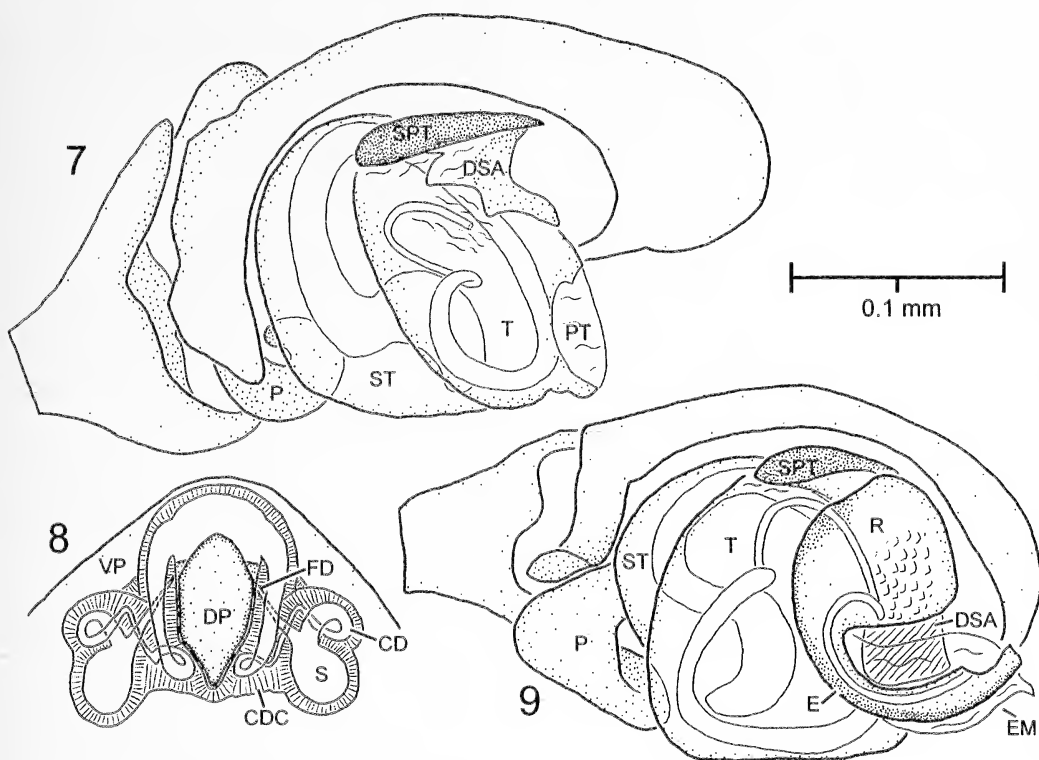


Figures 1–6.—Palpus of male *Carorita hiberna* from Thomas Ridge, North Carolina. 1. Embolic division, dorsal view; 2. Ventral view with embolic division removed; 3. Ventral view; 4. Mesal view; 5. Ectal view; 6. Palpal tibia, dorsal view. *Abbreviations:* DRP, dorsal radical process; DSA, distal suprategular apophysis; E, embolus; EM, embolic membrane; ETP, ectal tibial process; F, funulus; P, paracymbium; PT, prottegulum; PTA, palpal tibial apophysis; R, radex; SD, sperm duct; SPT, suprategulum; ST, subtegulum; T, tegulum; TP, radical tail piece.

1000. Trees found by Hennig86 and NONA were imported into PAUP. NONA trees were saved using the “ksv*” command. PAUP will arbitrarily resolve polytomies in trees saved using the “sv” command in NONA. The solution set from all three programs (PAUP, Hennig86, and NONA) was combined. Duplicate trees were eliminated. The remaining

unique trees were then filtered to exclude polytomous trees when more highly resolved compatible trees were found (Coddington & Scharff 1996). This set of trees was re-weighted and the data re-analyzed in PAUP.

Results.—PAUP, Hennig86, and NONA and all found multiple trees of 236 steps (calculated after excluding uninformative charac-



Figures 7–9.—Genitalia of *Carorita* species. 7. Male palpus of *C. hiberna* from Thomas Ridge, North Carolina, mesoventral view with embolic division removed; 8, 9. *Carorita limnaea* from McLean New York; 8. Cleared epigynum, ventral view; 9. Male palpus, ventromesal view. Abbreviations: CD, copulatory duct; CDC, copulatory duct capsule; DP, dorsal plate of epigynum; DSA, distal suprategular apophysis; E, embolus; EM, embolic membrane; FD, fertilization duct; P, paracymbium; PT, protegulum; R, radix; S, spermatheca; SPT, suprategulum; ST, subtegulum; T, tegulum; TP, radical tail piece; VP, ventral plate of epigynum.

ters) with a consistency index (CI) of 0.377 and a retention index (RI) of 0.673. PAUP found 63 trees, Hennig86 found 33 trees, and NONA found 45 trees. A total of 78 unique most parsimonious trees were found. Of these, 24 trees were more highly resolved but otherwise compatible with other most parsimonious trees. All trees place *Carorita limnaea* sister to *Carorita hiberna*. A strict consensus of all most parsimonious trees has a trichotomy composed of the *Carorita* clade, *Asthenargus paganus* and *Gongylidiellum vivum*. This clade is part of an 11-tomy composed of various erigonine terminals and clades. Successive character weighting stabilizes on six trees. All six trees are 236 steps long under equal weights and were among the original set of 78 trees. Except for the additional taxa, this set of six trees is identical to the result found in Hormiga's (in press) original analysis. Dis-

agreement among the six trees is found in two places: the relationships among the linyphiines, micronetines and all other linyphiids and the relationships among *Drepanotylus* Holm 1945, *Sciastes* Bishop & Crosby 1938 and the "distal erigonines" clade. The "distal erigonines" clade is fully resolved and identical in all six trees. The "distal erigonines" clade features a monophyletic *Carorita* clade sister to *Gongylidiellum vivum*. *Sisicottus* remains in the position reported by Zujko-Miller (1999), sister to *Oedothorax gibosus* (Blackwall 1841).

Implications.—The two species which formerly composed *Carorita* have traditionally been united based on their chaetotaxy (especially the presence of a prolateral macroseta on tibia I), the large paracymbium, the form of the suprategular apophysis, overall palpal conformation, the general form of the palpal

tibia, the relatively long tarsi, and proportional characteristics of the eyes (Duffey 1971; Millidge 1977). Millidge (1977) considered *C. limnaea* and *C. paludosa* Duffey 1971 to be members of a monophyletic group despite conspicuous differences in the form of the embolic division and cited it as evidence of how greatly the embolic division can vary within an otherwise "good" genus. Unfortunately, I have been unable to test this claim since I have not been able to examine specimens of *C. paludosa* and existing descriptions and illustrations are not adequate for scoring many of the characters in the matrix.

Optimization.—This analysis indicates that the genus *Carorita* can be defined phylogenetically on the basis of two unambiguous synapomorphies: the presence of a radical tailpiece (character 21) and the loss of a lamella characteristica (character 27). Although *C. paludosa* has a large mesal sclerite of the embolic division (Millidge 1977, fig. 159), I have been unable to determine from published descriptions whether it is a radical tailpiece or a lamella characteristica. Five characters can be optimized to provide additional support for the monophyly of *Carorita*. However, these five characters could also be placed on alternative tree nodes without affecting tree length. These are the presence of papillae on the protégulum (character 9; unknown in *C. paludosa*), a long embolus (character 17; short in *C. paludosa*), the shape of the radical tailpiece (character 22; unknown in *C. paludosa*), encapsulation of the epigynum (character 38; unknown in *C. hiberna* and *C. paludosa*), and a tuberculate radical tailpiece (character 74; unknown in *C. paludosa*). Although *C. limnaea* and *C. hiberna* are the only taxa in the analysis with a tuberculate radical tailpiece, their two closest relatives, *Asthenargus paganus*, and *Gongylidiellum vivum*, both lack a radical tailpiece and were therefore coded as inapplicable for this character. A generic revision of *Carorita* with a strong phylogenetic component should be undertaken in the near future to address the placement of *C. paludosa*.

All three *Carorita* species feature a strong kink or loop in the path of the sperm duct in the tegulum near the junction between the tegulum and the suprategulum (Figs. 7, 9; Millidge 1977, fig. 159). Most other erigonines have a sperm duct that follows a smooth curve

through the tegulum. However, when I attempted to code this as a cladistic character, I found a spectrum of conditions rather than a small number of discrete character states. Nevertheless, the presence of a kink in the sperm duct is a useful part of the diagnosis of *Carorita*.

Missing data.—Attributes of the tracheal system have long been relied upon as characters in linyphiid classification (Blest 1976; Millidge 1984, 1986). Hormiga (in press) demonstrated that these characters have high consistency. This analysis optimizes *C. hiberna* as having the haplotracheate condition, although no observation of the tracheal system of *C. hiberna* has been made. If *C. hiberna* is speculatively coded as having the desmitracheate condition (1: character 51) with no taenidia (0: character 52), 328 unique most parsimonious trees of 237 steps result (192 trees in Hennig86, 246 trees each in NONA and PAUP; CI = 0.376, RI = 0.670).

A total of 102 of these trees are more resolved than otherwise compatible trees. The strict consensus of these 102 trees has little phylogenetic structure. It features a polytomy of 21 clades and individual taxa at the node which represents the Erigoninae. *Carorita limnaea* and *C. hiberna* are not consistently monophyletic and form two of the branches in this 21-tomy. Successive character weighting of these 102 trees stabilizes on 30 trees (CI = 0.372, RI = 0.666). These trees are two steps longer under equal weights than the most parsimonious trees. The strict consensus of these 30 trees forms a topology unlike that found by Hormiga (1999), especially in the deep nodes. *Carorita limnaea* and *C. hiberna* form a paraphyletic assemblage rather than a monophyletic group. Under the assumption that *C. hiberna* is haplotracheate rather than desmitracheate without taenidia, the data are found to be more internally consistent and the resulting phylogenetic hypothesis that is consistent with the previous hypothesis (Hormiga in press), one which suffered from few missing observations.

DISCUSSION

Phylogenetic hypotheses can be communicated either implicitly as higher taxonomic names or explicitly in the form of a cladogram. If taxonomy is to reflect phylogenetic history, genera should serve as implicit hy-

pothesis that a particular group of species share a unique common ancestor. However, monotypic genera do not provide this grouping information and thus cannot be considered phylogenetic hypotheses. On the other hand, cladistic analyses by their nature explicitly convey detailed phylogenetic hypotheses. The ranks and labels assigned to nodes in a cladogram are less critical since the hypothesis of relationships is fully expressed in the tree. As part of an explicit phylogenetic hypothesis, detailed grouping information is available and monotypic genera are less problematic.

The placement of *Carorita hiberna* was difficult because of the many apparently autapomorphic character states exhibited by this species. However, no matter how many autapomorphic character states are found in a particular species, it must still have a sister taxon (Platnick 1976). Placing *Carorita hiberna* in a new monotypic genus without identifying its putative sister taxon would have been an abdication; a lack of a grouping hypothesis. As it stands, my circumscription of *Carorita* is based on explicit evidence and is subject to falsification given sufficient new evidence. Although these conclusions reflect the best available evidence, missing data has led to the optimization of some character states based on inference (Platnick et al. 1991). When additional specimens are discovered, the predictions of this analysis should be tested.

Between 1981 and 1995, over 70% of new linyphiid genera have been monotypic (Platnick 1989, 1993, 1997). The volume of new monotypic genera generated within the Linyphiidae indicates a critical lack of phylogenetic consideration. A phylogenetic approach based on morphological characters demands careful examination of comparative anatomy but the result is a rich hypothesis not only of taxonomic relationships but of character evolution. A broad phylogenetic context will be very helpful for associating monotypic genera with their relatives. This will no doubt lead to the synonymization of many existing genera. Ultimately, the utility of the linyphiid taxonomic system will be greatly improved. However, I have attempted to demonstrate that we do not need to wait for some grand phylogenetic hypothesis of the Linyphiidae. The basic context for applying phylogenetic criteria to new work in linyphiid systematics is already available.

TAXONOMY

Carorita Duffey & Merrett 1963

Carorita Duffey & Merrett 1963:573–576, figs. 1–8 (♂, ♀). Duffey 1971: 14–15, figs. 1–8 (♂, ♀). C Locket, Millidge & Merrett 1974: 92–94, figs. 56a–g (♂, ♀). Blest 1976: 188. Millidge 1977: 40, figs. 158, 159 (♂); 1984: 245–246. Brignoli 1983: 328. Roberts 1987: 108, figs. 53d, 53e (♂, ♀). Platnick 1989: 223; 1993: 252; 1997: 328. Heimer & Nentwig 1991: 124, figs. 352.1–353.4 (♂, ♀). Type species by original designation and by monotypy, *Oedothorax limnaeus* Crosby & Bishop 1927: 149–150, figs. 11–14.

Diagnosis.—Males of *Carorita* can be distinguished from most other erigonines by the form of the suprategulum which has a distinct boundary at its origin and by the kinked or looped path of the sperm duct through the tegulum (Figs. 7, 9). They are distinguished from males of other erigonines with these character states by the absence of a lamella characteristica and the presence of a radical tail piece (uncertain in *C. paludosa*). Females can be distinguished from other erigonines by the complex, anteriorly-projecting looped path of the copulatory ducts (Fig. 8).

Description.—Tibial macrosetae 2-2-1-1 (except in *C. hiberna*: 2-2-2-1); Tm IV absent. Tibia I with one distal prolateral macroseta (absent in *C. hiberna*). At least in *C. limnaea*, chelicerae with imbricated stridulatory files and median tracheal trunks unbranched, shorter than laterals, confined to abdomen (Blest 1976; haplotracheate *sensu* Millidge 1984). **Males:** Palpal tibia with one prolateral and one retrolateral trichobothrium. *Carorita limnaea* and *C. hiberna* (but not *C. paludosa*) with long embolus in frontal plane, radix with tuberculate tailpiece and no anterior radical process (Figs. 3, 9). Distal part of cymbium and ectal side of palpal tibia with clusters of macrosetae. **Females:** Females of *C. paludosa* have not been examined and details of female genitalia cannot be unambiguously interpreted using published descriptions and illustrations; females of *C. hiberna* unknown; females of *C. limnaea* with posteriorly oriented ventral plate invagination leading to copulatory openings; copulatory ducts encapsulated with loop at anterior maximum and again posterior to spermathecae near junction. Fertilization ducts project posteriomesally from spermathecae (Fig. 8).

Composition.—Three species: *Carorita limnaea* (Crosby & Bishop 1927), *C. paludosa* Duffey 1971 and *C. hiberna* (Barrows 1945).

Distribution.—North America (*C. limnaea*, *C. hiberna*) and Europe (*C. limnaea*, *C. paludosa*).

Carorita hiberna (Barrows 1945)

NEW COMBINATION

Figs. 1–7

Sisicottus hibernus Barrows 1945: 74, figs. 1, 2 (♂).
Brignoli 1983: 356.

Type.—Male holotype from United States: North Carolina, Great Smoky Mountains National Park, Mingus Creek, 1 February 1943, in OSU, examined.

Diagnosis.—Males of *C. hiberna* are readily distinguished from other *Carorita* species by the unusual, complex shape of the embolus which runs in a more or less frontal plane (Fig. 3E), by their long, ectally projecting, tuberculate, radical tailpiece (Fig. 3TP), by the horn-like process on the ectal side of the palpal tibia (Fig. 6ETP), by the presence of a distal macroseta on tibia III, by the absence of a prolateral macroseta on tibia I, and by the presence of a dorsal radical process (Fig. 1, DRP).

Description.—*Male*: (from Thomas Ridge, North Carolina). Carapace length = 0.6 mm. Tibial macrosetae weak; 2-2-2-1; Tm I = 0.34. Chelicerae with 5–6 promarginal teeth; 5 retromarginal teeth with proximal 2 larger than distal 3. Embolus describing a semicircular arc in more or less frontal plane with outside of curve ectal; tip of embolus arched in nearly transverse plane with outside of curve dorsal (Figs. 1, 3E). Embolic membrane long, narrow, curved with outside ectal (Fig. 2EM). Radix with anteriomesally projecting tuberculate tailpiece (Fig. 3TP) and ectodorsally projecting dorsal radical process (Fig. 1DRP). Protegulum on ectal side of bulb (Fig. 2PT). Palpal tibia with long, straight apophysis with flat distal margin; horn-like process on ectal side of apophysis; ectal and mesal sides of palpal tibia both with regions of semitransparent chitin (Figs. 4–6). *Female*: Unknown.

Distribution.—Known only from the Great Smoky Mountains National Park, North Carolina.

Material examined.—UNITED STATES:

North Carolina: Swain County, Great Smoky Mountains National Park, Mingus Creek, 1 February 1943, 1♂, (holotype, Barrows, OSU); Swain County, Great Smoky Mountains National Park, Thomas Ridge, ca. 200 m from trailhead at route 441, west-facing slope below trail, 4540 feet, old growth mixed hardwood, UTM: E3107, N39436, 22 September 1994, 1 m² litter sample, 1♂, (Cribbs team, GSMNP); Haywood County, Great Smoky Mountains National Park, Cataloochee, 150 m south of mouth of Palmer Branch at Caldwell Fork, 2800–3000 feet, old growth hemlock, UTM: E3107, N39436, 23–31 March 1997, pitfall trap, 1♂, (Coyle, Edwards & Wright, GSMNP) North Carolina, Great Smoky Mountains National Park.

Natural history.—*Carorita hiberna* is known only from three male specimens collected in the Great Smoky Mountains National Park. The rarity of this species in the face of intensive collecting efforts by Dr. Frederick Coyle (Western Carolina University) and his collaborators within the park raise questions about the long term prospects for the continued survival of this species. The rare diplurid spider *Microhexura montivaga* Bishop & Crosby 1925 is known only from spruce and Fraser fir forests in the southern Appalachians and is currently listed as a federally protected endangered species (Coyle 1981; Fridell 1995). The staphylinid beetle *Dasycerus bicolor* Wheeler & McHugh 1994 and the linyphiid spider *Sisicottus montigenus* Bishop & Crosby 1938 are both endemic to this same region and habitat type, have experienced recent and dramatic declines in their populations, and may be worthy of similar protected status (Wheeler & McHugh 1994; Zujko-Miller 1999). However, *C. hiberna* has been found in both mixed hardwood and hemlock forests. It does not appear to be associated with the declining spruce-fir habitat and though rare, there is no evidence that its population has actually declined since its discovery.

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^aTOWARDS A PHYLOGENY OF ENTELEGYNE SPIDERS (ARANEAE, ARANEOMORPHAE, ENTELEGYNAE)

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ABSTRACT. We propose a phylogeny for all entelegyne families with cribellate members based on a matrix of 137 characters scored for 43 exemplar taxa and analyzed under parsimony. The cladogram confirms the monophyly of Neocribellatae, Araneoclada, Entelegynae, and Orbiculariae. Lycosoidea, Amaurobiidae and some included subfamilies, Dictynoidea, and Amaurobioidea (sensu Forster & Wilton 1973) are polyphyletic. Phyxelidinae Lehtinen is raised to family level (Phyxelididae, NEW RANK). The family Zorocratidae Dahl 1913 is revalidated. A group including all entelegynes other than Eresoidea is weakly supported as the sister group of Orbiculariae.

The true spiders or Araneomorphae (*araneae verae* of Simon 1892) comprise more than 30,000 described species. The classification of this group has undergone a revolution in the last 30 years, sparked by Lehtinen's (1967) comprehensive reassessment of araneomorph relationships and steered by Hennig's phylogenetic systematics (Hennig 1966; Platnick & Gertsch 1976). Spider classification, portrayed by some authors as chaotic (Head 1995; Elgar et al. 1990; Vollrath & Parker 1997; Prenter et al. 1997) is actually one of the better-understood megadiverse orders (Coddington & Levi 1991): including the results reported here, 100 of the 108 currently recognized families (93%) have been placed cladistically, that is, in a higher taxon based on evidence assessed phylogenetically. New character systems compared across worldwide samples of taxa have led to many new and thought-provoking hypotheses in araneomorph phylogeny. The strongest test of such hypotheses is how simply they can account for the available data, i.e., most parsimonious cladograms based on matrices of taxa by characters. Tests specifically designed at the family level and above are increasingly common:

Raven (1985) and Goloboff (1993a) for Mygalomorphae (15 families); Coddington (1986, 1990a, b) for Orbiculariae (13 families) and Entelegynae; Platnick et al. (1991) on haplogynes (17 families) and Araneomorphae; Griswold et al. (1994, 1998) for Araneoidea (12 families), and Griswold (1993) for Lycosoidea and related families (11 families).

The latter studies targeted large but relatively well-defined lineages. It is now feasible to probe how these large lineages are related. We chose exemplars from all cribellate families, reasoning that taxa retaining this plesiomorphic feature are more likely to straddle the basal nodes of the phylogeny of higher groups than are their relatives that have lost the cribellum: therefore they are most likely to reflect phylogenetic groundplans. Although phylogenetically ancient, the cribellum is a complex feature unlikely to have evolved more than once. Most major araneomorph clades have cribellate members (exceptions are Palpimanoidea and Dionycha). A phylogeny of these basal taxa should mirror the relationships of the large clades they exemplify. As Lehtinen (1967: 202) declared, "because of the central position of the Cribellate groups in Araneomorphae, a detailed revision of them is a short cut to a rough classification of the whole suborder."

^aPresented as part of a symposium on "Higher Level Phylogenetics of Spiders."

A parsimonious cladogram based on an explicit taxon-character matrix is concise, logical, and testable. Our analysis tests many suprafamilial hypotheses of the last 30 years and is the first attempt to relate them using quantitative phylogenetic techniques: Amaurobioidea (*sensu* Forster & Wilton 1973), Amaurobiidae and included subfamilies (*sensu* Lehtinen 1967), Dictynoidea and Desidae (*sensu* Forster 1970), Entelegynae (*sensu* Coddington 1990b; Coddington & Levi 1991), Lycosoidea (Homann 1971; *sensu* Griswold 1993); Orbiculariae (*sensu* Coddington 1986, 1990a, b); and the 'RTA clade' (*sensu* Coddington & Levi 1991).

TAXA AND CHARACTERS

Table 1 comprises 43 exemplars from 21 of the 22 araneomorph families with cribellate members. As outgroups we included HYPOCHILIDAE (*Hypochilus*), AUSTROCHILIDAE (*Hickmania* and *Thaida*), and FILISTATIDAE (*Filistata* and *Kukulcania*, Filistatinae). From eresoids, we included OECOBIIDAE (*Oecobius* and *Uroctea*) and ERESIDAE (*Eresus* and *Stegodyphus*). From Orbiculariae we included DEINOPIIDAE (*Deinopsis* and *Menneus*), ULOBORIDAE (*Octonoba* and *Uloborus*) and an araneoid groundplan. Recent phylogenetic study of this superfamily (Griswold et al. 1998) gives us confidence that the reconstructed groundplan accurately reflects the primitive conditions for Araneoidea. From "dictynoids" we included DICTYNIDAE (*Dictyna* and *Nigma*, *Lathys*, and *Tricholathys* representing Dictyninae, Cicurinae, and Tricholathysinae, respectively), DESIDAE (*Badumna candida*, *B. longinquua*, and *Matachia*, formerly Matachiinae), and NICODAMIDAE (*Megadictyna*). From "amaurobioids" we included AMAUROBIIDAE (*Amaurobius* and *Callobius* (Amaurobiinae), *Metaltella* (Metaltellinae), *Retiro* and *Pimus* (Macroibuninae), *Phyxelida*, *Vytfutia*, and *Xevioso* (Phyxelidinae)), AMPHINECTIDAE (*Maniho*), NEOLANIDAE (*Neolana*), AGELENIDAE (*Neoramia*), and TITANOECIDAE (*Goeldia* and *Titanoeca*). From lycosoids and related groups we included CTENIDAE (*Acanthoctenus*), MITURGIDAE (*Raecius* and *Uduba*, Uliodoninae), PSECHRIDAE (*Psechrus*), STIPHIDIIDAE (*Baiami* and *Stiphidion*); TENGELLIDAE (*Tengella*), and ZOROPSIDAE (*Zoropsis*).

We omitted Gradungulidae because the cribellate genera are extremely rare in collections and its placement in Austrochiloidea seems firm (Forster, Platnick & Gray 1987; Platnick et al. 1991). Voucher specimens for exemplars are deposited in the California Academy of Sciences (CAS) with the exception of *Vytfutia* (Deeleman coll.) and male *Raecius* (NHMV). Character data taken from the literature include the suite of classical characters from spider internal anatomy (characters 43–49: Platnick 1977; ex Millot 1931, 1933, 1936; Marples 1968 [these have been recorded for hypochiloids, austrochiloids, and such a wide variety of haplogyne and entelegyne Araneoclada that we are confident that the assumed states for entelegyne exemplars in Table 1 are justifiable]) and character 114, presence/absence of the muscle M29 in the male palp (assumed for all taxa in Table 1 following Huber 1994). Silk ultrastructure data are taken from Eberhard & Pereira (1993) and from unpublished observations (R. Carlson in lit.).

Characters, character states, and codings are listed in Table 1. Some features are most succinctly described by reference to a taxon for which they are typical, e.g., 'dictynid conductor.' For figures of entelegyne genitalia see especially Lehtinen (1967), Coddington (1990a) and Griswold (1993); for features of spinnerets see especially Platnick et al. (1991) and Griswold et al. (1998). Character evolution is summarized on the cladogram (Fig. 1) optimized via Clados (Nixon 1992) and MacClade (Maddison & Maddison 1992).

METHODS AND ANALYSIS

Spigot classification follows Coddington (1989); all specimens were critical point dried before scanning electron microscope (SEM) examination of spinning organs. Behavioral observations were made on living animals in the field or lab.

The matrix (all characters unordered and equally weighted) was analyzed with three phylogenetic packages: Nona 1.6 (Goloboff 1993b), Hennig86 1.5 (Farris 1988), and Pee-Wee 2.6 (Goloboff 1997), using a wide variety of randomized and directed search strategies. Nona (using both 'amb =' and 'amb-' options for clade support) and Hennig86 found the same three topologies, including Fig. 1 (length 376, ci 0.43, ri 0.69). The two alternate topologies involved local rearrangements of Ni-

codamidae and Eresoidea. The strict consensus has one 4-tomy at the entelegyne node, otherwise identical to Fig. 1.

We used successive and implied weighting (Carpenter 1988; Goloboff 1993c) to further evaluate the data. Successive weighting in Nona (length 16,346, ci 0.63, ri 0.80) preferred Fig. 1. Successive weighting in Hennig86 (length 1127, ci 0.79, ri 0.88) found Fig. 1 as well as two other trees one step longer. Pee-Wee at concavity functions of 3 and 4 (fits 962.6 and 1009.0, length 378) found one tree in which *Retiro* and *Pimus* swapped places, otherwise identical to Fig. 1. Concavity 5 (fit 1041.6, lengths 376, 378) found Fig. 1 as well as the tree found at concavities 3 and 4. Concavity 6 (fit 1067.8, length 376) found only Fig. 1. Because Fig. 1 was the only topology judged optimal by all criteria (equal, successive, and implied weights), we recommend it as the working hypothesis for entelegyne relationships. Table 1 gives the number of steps, consistency index, retention index, weight (*ex* Hennig86), and fit (*ex* Pee-Wee, concavity 4) for all characters on Fig. 1.

In addition to mapping character support at nodes, we also examined cladogram robustness with branch support indices (Bremer 1994) calculated with Nona using the parameters 'h25000; bsupport8;'. The "Bremer Support" ("Decay Index") for a given node in the shortest unconstrained tree is the num-

ber of additional steps required in the shortest trees for which that node collapses. The following Bremer Support values were found for the clades on Fig. 1: Austrochiloidea (5), Araneoclada (1), Entelegynae (1), Haplogynae (8), Eresoidea (1), *Stegodyphus-Eresus* (8), *Uroctea-Oecobius* (4), Canoe Tapetum Clade (0), Orbiculariae (2), *Deinopis-Octonoba* (3), *Deinopis-Menneus* (4), *Uloborus-Octonoba* (5), *Megadictyna-Zoropsis* (0), Divided Cribellum Clade (1), Titanocoids (1), *Titanoeca-Goeldia* (2), *Vytfutia-Phyxelida* (2), *Xevioso-Phyxelida* (2), RTA Clade (1), Dictynidae (2), *Tricholathys-Nigma* (1), *Dictyna-Nigma* (3), Amaurobioids (1), Fused Paracribellar Clade (2), Stiphidioids (1), *Stiphidion-Baiami* (5), Agelenoids (2), *Maniho-Badumna c* (2), *Maniho-Metaltella* (2), Desidae (1), *Badumna l-Badumna c* (5), *Retiro-Zoropsis* (1), Amaurobiidae (1), *Pimus-Callobius* (2), *Amaurobius-Callobius* (3), *Tengella-Zoropsis* (4), *Raecius-Zoropsis* (2), *Raecius-Uduba* (2), Lycosoidea (2), and *Acanthoctenus-Zoropsis* (3).

RESULTS

Status of the Lycosoidea and their kin.—

Homann (1971, followed by Levi 1982) defined the Lycosoidea on the basis of a grate-shaped tapetum in the indirect eyes. Griswold (1993) produced a phylogeny for those families plus selected tengellids and miturgids that

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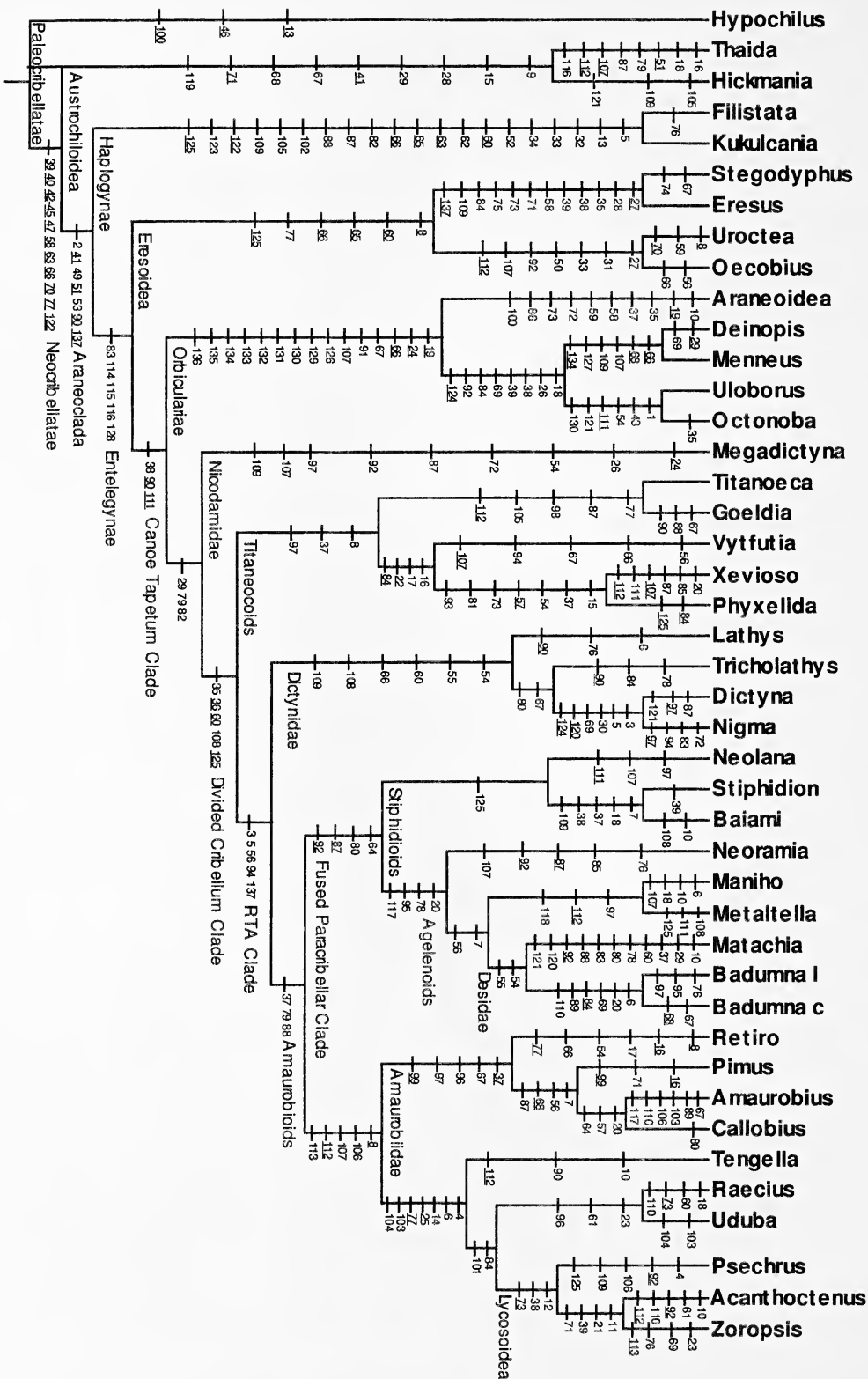
Table 1.—Character by taxon matrix. Rows represent characters. The first state listed is coded as "0", the second as "1", etc., "?" = unknown, "-" = non-applicable. Columns represent taxa. The final five columns give the number of steps, the consistency index, the retention index, weight, and fit on Fig. 1. Taxon abbreviations are Ac = *Acanthoctenus*; Am = *Amaurobius*; AP = Araneoidea; Ba = *Baiami*; Bd = *Badumna candida*; Ca = *Callobius*; De = *Deinopis*; Di = *Dictyna*; Er = *Eresus*; FP = *Filistata*; Go = *Goeldia*; Hi = *Hickmania*; Hy = *Hypochilus*; Ix = *Badumna longinquua*; Ku = *Kukulcania*; La = *Lathys*; Ma = *Matachia*; Me = *Megadictyna*; Mh = *Maniho*; Mn = *Menneus*; Mt = *Metaltella*; Ne = *Neoramia*; Ni = *Nigma*; Nl = *Neolana*; Oc = *Octonoba*; Oe = *Oecobius*; Ph = *Phyxelida*; Pi = *Pimus*; Ps = *Psechrus*; Ra = *Raecius*; Re = *Retiro*; Sg = *Stegodyphus*; St = *Stiphidion*; Te = *Tengella*; Th = *Thaïda*; Ti = *Titanoeca*; Tr = *Tricholathys*; Ud = *Uduba*; Ul = *Uloborus*; Ur = *Uroctea*; Vy = *Vytfutia*; Xe = *Xevioso*; Zo = *Zoropsis*.

Character abbreviations: ALS = anterior lateral spinnerets; annul. = annulate; C = conductor; cent. = central; CR'ed = cut and reeled; dict = dictynid; E = embolus; embr. = embraces; extra = in addition to C and MA; iL1 = inside first leg; iL4 inside fourth leg; long. = longitudinal; L3 = third leg; L4 = fourth leg; MAP = major ampullate; mAP = minor ampullate; membr. = membraneous; met = metal-telline; Oe = oecobiid; oL1 = outside first leg; opp. = opposite; papill. = papillate; PMS = posterior median spinnerets; post. = posterior; PY = pyriform; scl. = sclerotized; spinn. = spinneret; STP = sclerotized tegular process; squam. = squamate; strob. = strobilate; Th = *Thaïda*; trans. = transverse; trich. = trichobothria; Ulo = uloborid.

Table 1.

		HTHFKSEUODMUCAMONTLGVCKPNSBNMBIRPACTRUPZA					
Legs		yhiugrreenlcPeiiraioyehltaehtadxmaeadsoc	St	CI	RI	Wt	Fit
1.	Femoral trichobothria: absent; present;	0000000000011000000000000000000000000000	1	1.00	1.00	10	10
2.	Tarsal organ: exposed; capsulate;	0001111111111111111111111111111111111111	1	1.00	1.00	10	10
3.	Tarsal trichobothria: absent; present;	000000000000000000011000001111111111111111	2	.50	.95	4	8
4.	Tarsal trichobothrial rows: 1; 2+;	-----00-----0000000000000111011	2	.50	.75	3	8
5.	Metatarsal trichobothria: 1-2; >2;	00011000000000000110000011111111111111111	3	.33	.89	2	6.6
6.	Tarsal trichobothria: normal; longer distally;	-----10-----111011001111000000	4	.25	.66	1	5.7
7.	Palpal tibial trichobothria: absent; present;	0000000000? 0? 00000000000110111101100000	3	.33	.77	2	6.6
8.	Trich. base: smooth; trans. ridge; long. ridge;	00000110100000000001111100? 0000000111111111	5	.20	.75	1	5
9.	Trichobothrial base: simple; notched;	0110000000000000000000000000000000000000	1	1.00	1.00	10	10
10.	Trochanteral notch: absent; present;	0000000000000100000000000010101000000100001	6	.16	.00	0	4.4
11.	Tarsal claws: 3; 2;	0000000000000000000000000000000000000011	1	1.00	1.00	10	10
12.	Claw tufts: absent; present;	0000000000000000000000000000000000000111	1	1.00	1.00	10	10
13.	Calamistral rows: 2; 1; 3;	0112211-11111-1111111111111111111111111111-111111	2	1.00	1.00	10	10
14.	Calamistram: linear; oval;	0000000-00000-0000000000000000000000000000000111111	1	1.00	1.00	10	10
15.	Calamistram origin: basal; median;	0110000-00? 00-000000001100000000000000000000	2	.50	.66	3	8
16.	Male palpal femoral thorns: absent; present;	010000000000000000000001110000000001100000000	4	.25	.40	1	5.7
17.	Female palpal femoral thorns: absent; present;	000000000000000000000001110000000001000000000	2	.50	.66	3	8
18.	Feathery hairs: absent; present;	0100000001111000000000000011010000000010000	5	.20	.50	1	5
19.	Hair: plumose; pseudoserrate; serrate;	00000000011112000000000000000000000000000000	2	1.00	1.00	10	10
20.	Metatarsal preening combs: absent; present;	00000000000000000000000100001111000011000000	4	.25	.50	1	5.7
21.	Tibial ventral spine number: <7; >7;	0011	1	1.00	1.00	10	10
22.	Male metatarsus I: unmodified; modified;	0000000000000000000000011100000000000000000	1	1.00	1.00	10	10
23.	Male tibial crack: absent; present;	0000000000000000000000000000000000000011010	2	.50	.50	2	8
24.	Serrate accessory claw setae: absent; present;	00000000011111000000000000000000000000000000	2	.50	.80	4	8
25.	Female posterior leg scapula: absent; present;	0000000000? 00000000000000000000000000000111111	1	1.00	1.00	10	10
26.	Deinopoid tarsal comb: absent; present;	000000000111010000000000000000000000000000	2	.50	.75	3	8
		HTHFKSEUODMUCAMONTLGVCKPNSBNMBIRPACTRUPZA					
Carapace		yhiugrreenlcPeiiraioyehltaehtadxmaeadsoc	St	CI	RI	Wt	Fit
27.	Carapace shape: oval; square; round;	00000112200000000000000000000000000000000	2	1.00	1.00	10	10
28.	Clypeal hood: absent; present;	011001100000000000000000000000000000000000	2	.50	.66	3	8
29.	Thickened setae at fang base: absent; present;	011000000? 00011111111111111011111111111111	4	.25	.70	1	5.7
30.	Male chelicerae: normal; bowed;	000000000000000100000000000000000000000000	1	1.00	1.00	10	10
31.	Chelicerae: normal; small;	000000011000000000000000000000000000000000	1	1.00	1.00	10	10
32.	Chelicerae: free; fused at base;	000110000000000000000000000000000000000000	1	1.00	1.00	10	10
33.	Cheliceral teeth: present; absent;	0001100110000000000000000000000000000000000	2	.50	.66	3	8
34.	Cheliceral chela: absent; present;	000110000000000000000000000000000000000000	1	1.00	1.00	10	10
35.	Cheliceral boss: absent; present;	0000011000? 01101111111111111111111111111111	4	.25	.66	1	5.7
36.	Cheliceral boss: small; large;	-----00---? -00-11111111111111111111111111111111	1	1.00	1.00	10	10
37.	Chilum: absent; median; bilateral;	0? ? 00? ? 00? ? ? 020? 00? 1112221? ? 22122? ? 11222222	7	.28	.68	1	4.4
38.	Tapetum: primitive; canoe; grate; absent;	000003300333311111111111111111111111111111122	5	.60	.86	5	6.6
39.	Posterior eye row: straight; recurved;	0111001100001111111111111011111111111111111100	5	.20	.55	1	5
40.	Serrula tooth rows: multiple; single;	011	1	1.00	1.00	10	—
41.	Sigilla: present; absent;	0110011	2	.50	.50	2	8
42.	Medial cheliceral concavity: present; absent;	011	1	1.00	1.00	—	—
43.	Venom gland: cheliceral; carapace; absent;	01111111112211111111111111111111111111111111	2	1.00	1.00	10	10
44.	Coxal gland duct: convoluted; simple;	011	1	1.00	1.00	—	—
45.	5th endosternite invagination: present; absent;	011	1	1.00	1.00	—	—
46.	Midgut cheliceral diverticula: present; absent;	011	1	1.00	1.00	—	—
47.	Pharynx muscle origin: carapace; rostrum;	011	1	1.00	1.00	10	—
		HTHFKSEUODMUCAMONTLGVCKPNSBNMBIRPACTRUPZA					
Abdomen		yhiugrreenlcPeiiraioyehltaehtadxmaeadsoc	St	CI	RI	Wt	Fit
48.	Intestine: M-shaped; straight;	000111	1	1.00	1.00	10	10
49.	Heart ostia number: 4; 3 or 2;	000111	1	1.00	1.00	10	10
50.	Anal tubercle: small; large;	000000011000000000000000000000000000000000	1	1.00	1.00	10	10
51.	Posterior spiracles: 2; 1;	01011	2	.50	.00	0	8
52.	Posterior spiracles: wide; narrow;	-1-0011	1	1.00	1.00	10	10
53.	Post. respiratory system: booklungs; tracheae;	00011	1	1.00	1.00	10	10
54.	Median tracheae: simple; branched;	-0---00000? 110111100011000000111000000000	6	.16	.58	0	4.4
55.	Lateral tracheae: simple; branched; absent;	-----00000? 0000222000000000000111000000000	2	1.00	1.00	10	10
56.	Epiandrous spigots: present; absent;	00? 0000010? ? ? 0011110? 100? ? 1000001000? 11? 11	5	.20	.66	1	5
57.	Epiandrous spigots: dispersed; 2 bunches;	00? 00000-0? ? ? 00---00-? -11?? ?-----011-----	2	.50	.66	3	8
		HTHFKSEUODMUCAMONTLGVCKPNSBNMBIRPACTRUPZA					
Spinneret morphology		yhiugrreenlcPeiiraioyehltaehtadxmaeadsoc	St	CI	RI	Wt	Fit
58.	Spinn. cuticle: annul.; ridged; squam.; papill.;	01111331111112111111111111111111111111111111	3	1.00	1.00	10	10
59.	Cribellum: present; absent;	000000010000010000000000000000000000000000	2	.50	.00	0	8
60.	Cribellum: entire; divided;	0001111-10000-0000011111111101111011101111	6	.16	.61	1	4.4
61.	Cribellate spigots: uniform; clumped;	00000? 0-00000-00000000000000000000000001001	2	.50	.50	2	8
62.	Cribellate spigots: strobilate; claviform;	0110010001111011011001100000000000000000000	1	1.00	1.00	10	10
63.	Tartipores: absent; present;	01100111111111111111111111111111111111111111	2	.50	.50	2	8
64.	ALS field margin: narrow; broad;	0000000000000000000000? 00111111110011000000	2	.50	.90	4	8
65.	ALS MAP: clustered; dispersed;	00011111-0000000000000000000000000000000000	2	.50	.75	3	8
66.	ALS MAP number: >3; 3; 2; 1;	0221100030033323332322222222222222222222222	9	.33	.60	2	4
67.	ALS MAP nubbin: absent; present;	0110010001111011011001100000000001101000000	19	.11	.50	0	3.3
68.	ALS MAP nubbin: one; extra;	-11--0---11000-000-00-00-----101-1-----	4	.25	.50	1	5.7
69.	ALS piriform margin: rounded; flat; sharp;	000000002111001100000000000000110000000020	5	.40	.57	2	5.7

[illegible]



shared with Lycosoidea a derived, oval cal-amistrum. Figure 1 corroborates the oval cal-amistrum (14) as a synapomorphy for this group. The former miturgid genera *Campos-tichomma*, *Zorocrates*, *Zorodictyna*, *Raecius*, and *Uduba* (clade BB in Griswold 1993) comprise the family Zorocratidae Dahl 1913. Synapomorphies of Zorocratidae are: male tibial crack (23), clumped cribellar spigots (61), and a male palpal tibial ventroapical process (96). Zorocratidae are sister to Lycosoidea (Fig. 1) based on posterior median spinnerets with many cylindrical spigots (84) and a dorsal scopula on the cymbium (101). Stiphidiidae (*Baiami* and *Stiphidion* in Fig. 1) were formerly included in Lycosoidea, but in this analysis are more closely related to the Agelenidae, Amphinectidae, Desidae, and Neolanidae, based on a suite of rather homoplasious characters. Perhaps the strongest evidence is the clumped rather than dispersed arrangement of the paracribellar spigots on the PMS (80). Jointly these characters overrule the grate-shaped tapetum, which therefore appears to have evolved independently in stiphidiids. Lycosoidea will probably be further modified by detailed study of lineages now included in Ctenidae.

Amaurobiidae and included subfamilies (*sensu* Lehtinen 1967).—Defined classically by a plesiomorphy (presence of the cribellum), perhaps Amaurobiidae was most obviously in need of relimitation after the collapse of the old Cribellatae. Lehtinen (1967) proposed nine subfamilies, seven of which are treated here: Matachiinae (*Badumna*, *Matachia*), Desinae (*Maniho*), Phyxelidinae (*Phyxelida*, *Xevioso*; also *Vytfutia* following Griswold 1990), Stiphidiinae (*Baiami*, *Stiphidion*),

Macrobuninae (*Pimus*, *Retiro*), Metaltellinae (*Metaltella*) and Amaurobiinae (*Amaurobius*, *Callobius*). The cribellate Altellopsinae are known only from females (Lehtinen 1967: 338) and Rhoicininae are neither cribellate nor amaurobiids (Griswold 1993). Unless the limits of the family are expanded to include the lycosoids, one must conclude that Amaurobiidae is the most seriously polyphyletic family discovered to date. Only Lehtinen's macrobunines (paraphyletic) and amaurobiines arguably remain in Amaurobiidae (Fig. 1). Lehtinen's desines and metaltellines are closely related and belong in Amphinectidae *sensu* Forster & Wilton 1973: this result corroborates Davies (1998). As noted above, Stiphidiidae *sensu* Forster & Wilton 1973 (*Stiphidion* and *Baiami* in Fig. 1) is sister to Neolanidae, not amaurobiids. Matachiines are desids *sensu* Forster & Wilton 1973 (Fig. 1); at least *Matachia* is strikingly similar to the ecribellate *Desis*. Phyxelidinae Lehtinen 1967 (formerly Amaurobiidae), which includes *Ambohima*, *Kulalania*, *Lamaika*, *Malaika*, *Matundua*, *Namaquarachne*, *Phyxelida*, *Pongolania*, *Themacrys*, *Vidole*, *Vytfutia* and *Xevioso*, constitutes a distinct family (Phyxelididae, NEW RANK). Phyxelididae (*Vytfutia*, *Xevioso* and *Phyxelida* in Fig. 1) is sister to Titanoecidae (*Titanoeca* and *Goeldia* in Fig. 1), not close to amaurobiids. Phyxelididae is corroborated by various synapomorphies: male (16) and female (17) palpal femur thorns, modified male metatarsus I (22), and long, narrow, closely packed and laterally flattened PMS paracribellar spigots (81).

Amaurobioidea and Dictynoidea (*sensu* Forster & Wilton 1973).—Building upon an extensive study of the respiratory systems of

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Figure 1.—Cladogram for entelegyne spider exemplars. Character changes are noted on branches by character number, with ambiguous optimizations underlined. Characters optimized at the neocribellate node are ambiguous because Mygalomorphae, Mesothela, and Amblypygi are not considered in this matrix. Taxon names are to the right of their branch. Familial assignments of exemplars on this cladogram are: AGELENIDAE (*Neoramia*), AMAUROBIIDAE (*Amaurobius*, *Callobius*, *Pimus*, and *Retiro*), AMPHINECTIDAE (*Maniho* and *Metaltella*), AUSTRORHILIDAE (*Hickmania* and *Thaïda*), CTENIDAE (*Acanthoctenus*), DEINOPIDAE (*Deinopsis* and *Menneus*), DESIDAE (*Badumna c[andida]*, *Badumna [longinquua]*, and *Matachia*), DICTYNIDAE (*Dictyna*, *Nigma*, *Lathys*, and *Tricholathys*), ERESIDAE (*Eresus* and *Stegodyphus*), FILISTATIDAE (*Filistata* and *Kukulcania*), HYPOCHILIDAE (*Hypochilus*), NEOLANIDAE (*Neolana*), NICODAMIDAE (*Megadictyna*), OECOBIDAE (*Oecobius* and *Uroctea*), PHYXELIDIDAE (*Phyxelida*, *Vytfutia*, and *Xevioso*), PSECHRIDAE (*Psechrus*), STIPHIDIIDAE (*Baiami* and *Stiphidion*), TENGELLIDAE (*Tengella*), TITANOECIDAE (*Goeldia* and *Titanoeca*), ULOBORIDAE (*Octonoba* and *Uloborus*), ZOROCRATIDAE (*Raecius* and *Uduba*), and ZOROPSIDAE (*Zoropsis*).

spiders, Forster (1970) and Forster & Wilton (1973) defined two superfamilies that contained all the families treated here as well as others. The Amaurobioidea (unbranched, slender tracheae) included Agelenidae, Amaurobiidae, Amphinectidae, Ctenidae, Cycloctenidae, Neolanidae, Psechridae, and Stiphidiidae. Figure 1 suggests a much more limited arrangement: Amaurobiidae is sister to only teggellids, zorocratids, and lycosoids. The Dictynoidea (at least median tracheae branched) included Amaurobioididae, Anyphaenidae, Argyronetidae, Cybaeidae, Dictynidae, Desidae, Hahniidae, and Nicodamidae. The unbranched condition (54) is primitive and thus Amaurobioidea should not be expected to be monophyletic. Branched tracheae (54), however, originates six times on Fig. 1 and although it helps to define families (Uloboridae, Dictynidae) it does not, as yet, clearly define a larger clade. Dictynidae is monophyletic and is sister (or part of the sister group) to most distal entelegynes, including Neolanidae, Stiphidiidae, Amphinectidae, Amaurobiidae, Desidae, Agelenidae, Teggellidae, Zorocratidae, and Lycosoidea.

The 'RTA' Clade.—Coddington & Levi (1991) suggested an informal but informative grouping for those spiders having a retrolateral tibial apophysis (RTA) on the male palp, including taxa thought to lack the RTA secondarily. A variety of tibial apophyses on the male palp exist, sometimes on the same animal, and here we code this diversity as four homologies rather than one. The RTA itself (94) still defines roughly the same lineage (Fig. 1), except that the absence of the RTA in Nicodamidae, Phyxelididae, and Titanocidae is primitive, not secondary and thus excludes them from the RTA clade. An additional unambiguous synapomorphy is trichobothria on the tarsi (3). *Vytfutia* apparently evolved the RTA independently.

Outgroup of the Orbiculariae.—With more than 10,000 described species and a great variety of documented webs and other behaviors, the Orbiculariae comprise one of the largest and most interesting clades of spiders. Coddington (1990b) implied Dictynoidea as a possible Orbicularian sister group. Platnick et al. (1991) suggested that the Amaurobioidea (represented in their study by *Amaurobius*) and Dictynoidea (represented by *Dictyna*) together could be the sister group.

Coddington & Levi (1991) suggested that the 'RTA clade' (including Dictynoidea, Amaurobioidea, Dionycha, and Lycosoidea) was the orbicularian sister group. The first two studies lacked many relevant taxa, and the last was a review, not a new analysis. This study omits palpimanoids, but suggests that the sister group to Orbiculariae is essentially all entelegyne spiders other than eresoids. In retrospect, the difficulty in finding the sister group of orbweavers is understandable. The answer, suggested by all of these studies in one way or another, is not one or a few classical families, or even any pre-existing taxonomic hypothesis in spiders. It is, rather, a previously unknown suprafamilial clade whose precise characterization still requires much work. In one alternative parsimonious topology for this dataset, however, the orbicularian sister group is Nicodamidae (*Megadictyna*), based on serrate accessory claw setae (24), the entire cribellum (60), and inverted posture in the web (125). Given this possibility, further field studies of nicodamid behavior and web construction would be welcome.

New entelegyne groups.—As before (Coddington & Levi 1991; Scharff & Coddington 1997; Griswold et al. 1998) we propose informal names for a few clades so that they may be discussed and tested by other workers prior to formal taxonomic recognition. All entelegynes distad of eresoids we call the "canoe-tapetum clade" (Fig. 1). On this cladogram the canoe tapetum arises unambiguously at this node and certainly represents an important restructuring of the spider visual system. The clade is also supported by the appearance of the modified silk spigot on the PLS (90), called the pseudoflagelliform in deinopoids, but now known to have homologs in many other lineages. This spigot presumably contributes additional axial fibers to the cribellate silk, as noted by Eberhard & Pereira (1993), and may represent an important event in the evolution of capture threads.

It seems logical to redefine the Amaurobioidea to include all families in the sister clade to Dictynidae (Fig. 1). Likewise, the clade including Titanocidae and Phyxelididae could be called the "titanocoids." "Agele-noids" could refer to Agelenidae, Amphinectidae, and Desidae.

Similarly it seems worthwhile to recognize the "fused paracribellar clade" as well as the

“divided cribellum clade” (Fig. 1). The functional role of paracribellar fibrils in capture threads is not known with certainty, but these taxa have the paracribellar shafts fused so that many spigots emerge from the same shaft—a striking morphology (80). The same clade is also defined by wide ALS piriform field margins (64)—another spinning field feature whose functional significance is still unknown. Likewise, the divided cribellum (60) is scarcely free from homoplasy, but one of its origins does define a large clade of spiders (Fig. 1).

DISCUSSION

These results constitute the most detailed proposal to date for basic entelegyne relationships. Added to previous analyses (refs. in Coddington & Levi 1991), 100 of the 108 current spider families are now placed in higher taxa intermediate between suborder and superfamily. *Incertae sedis* families are only Cryptothelidae, Cybaeidae, Cycloctenidae, Hahniidae, Halidae, Homalonychidae, the remaining Miturgidae, and Zodariidae. The higher taxa Palpimanoidea and Dionycha (if monophyletic) also need to be placed in the general schema. Both groups are entirely ecribellate and so many informative characters cannot be scored. Palpimanoidea was placed by Platnick et al. (1991) as sister group of the clade Orbiculariae plus the RTA clade, which group was supported by the presence of the PLS pseudoflagelliform gland spigot (90). Nothing in our additional data challenges this conclusion. On the whole, these results sharpen rather than contest earlier work by providing a much more detailed and factually based hypothesis for test.

A notable result is the unavoidable homoplasy in character systems traditionally relied upon in araneomorph classification. For example, branched median tracheae (54) arise six times, the divided cribellum (60) evolves three times and reverts to entire three times (Dictynidae, *Matachia* and *Raecius*). Loss and regain of epiandrous spigots (56) occurs. Although the median apophysis (109) is homologous wherever it occurs, eight unambiguous losses are required. Once again understanding spider phylogeny seems to be, as succinctly put by Coddington & Levi (1991: 575), “not so much a question of finding characters as it is of allocating homoplasy.” Spider data, however, is not abnormally homoplasious.

Based on regression coefficients calculated by Sanderson & Donoghue (1989) 43 taxa yield on average *ci* values of about 0.35; the value observed here (0.43) is rather better.

Several tasks remain before the first, rough, cladistic reconnaissance of Araneae could be said to be “complete.” The major groups Palpimanoidea (Forster & Platnick 1984) and Dionycha (sensu Coddington & Levi 1991) as well as families mentioned above, are not placed on this cladogram. At infrafamilial levels, many cribellate enigmas remain unstudied, e.g., *Poaka* (Psecridae?) and *Aebutina* (Dictynidae?). The generality of these results is uncertain because in many cases the monophyly of families containing cribellate and ecribellate members is untested (especially Agelenidae and Dictynidae). Nevertheless, in its breadth of taxa and characters this study represents progress towards a comprehensive family-level phylogeny for the true spiders.

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HYPOTHESES FOR THE RECENT HISPANIOLAN SPIDER FAUNA BASED ON THE DOMINICAN REPUBLIC AMBER SPIDER FAUNA

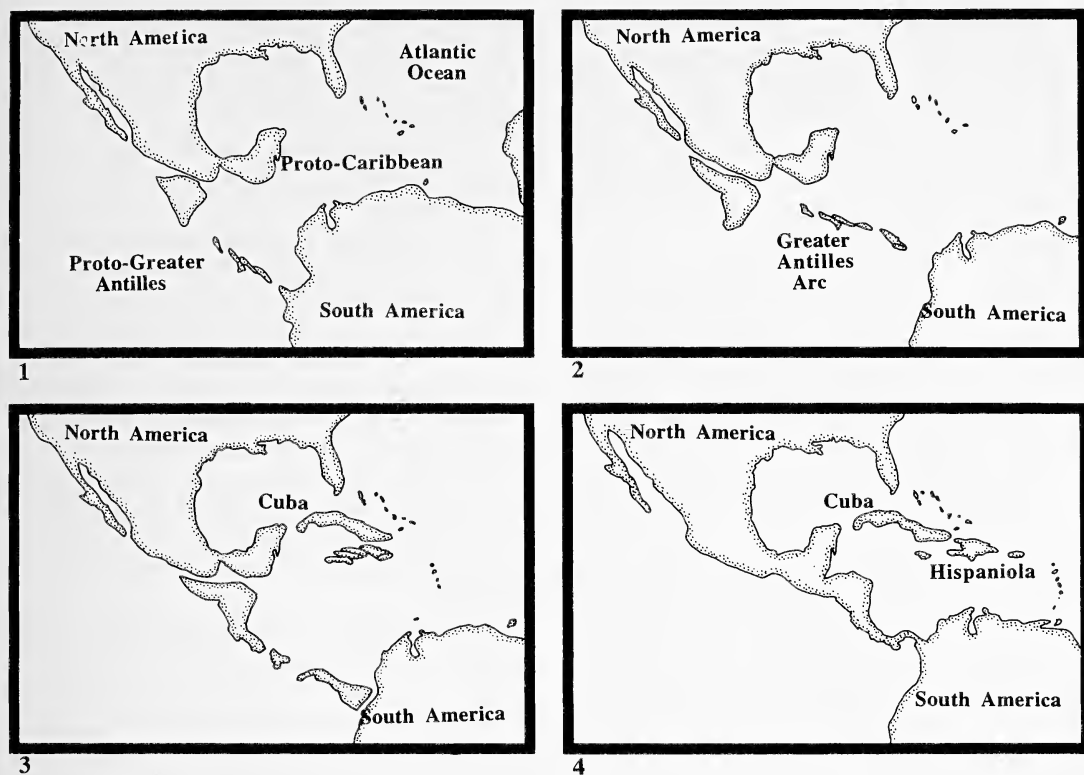
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ABSTRACT. The Dominican Republic amber fossil spider record is examined and hypotheses generated concerning the Recent Hispaniolan spider fauna which is, at present, poorly known. The families Cyrtacheniidae, Microstigmatidae, Nemesiidae, Ochyroceratidae, Tetrablemmidae, Palpimanidae, Hersiliidae, Symphytognathidae *s.l.*, Anapidae, Mysmenidae, and Hahniidae, known from the fossil, but not Recent, fauna are predicted to be components of the Recent fauna of Hispaniola. Based on a terrestrial invertebrate species longevity of less than ten million years, the presence of endemic and non-endemic species, and the assumption that Hispaniola has suffered no major ecological disruption that would cause the amber lineages to become extinct, the following hypotheses are made: Filistatidae and Desidae colonized Hispaniola after the Miocene amber formation; Drymusidae, Amaurobiidae, and Deinopidae were present on Hispaniola during the Tertiary, but avoided capture, or have yet to be found in the amber; and Scytodidae, Oecobiidae, Uloboridae, Dictynidae and Clubionidae have colonized Hispaniola since the Miocene amber formation but these families, which were present on Hispaniola during the period of amber formation, contain undiscovered endemic species.

Hispaniola is unique, in terms of its known spider fauna, in that more families are recorded from fossil species in Miocene Dominican Republic amber than are recorded from extant species (Wunderlich 1988; Penney 1999). Petrunkevitch (1928) considered the Greater Antillean spider fauna to represent an eastern outgrowth of the Central American fauna by way of a presumed earlier land connection and subsequent continent–island vicariance. However, a land connection appears not to have existed (Ross & Scotese 1988). Based on a quantitative computer model of plate tectonics, these authors proposed that the Proto-Greater Antillean (Fig. 1) and subsequently the Greater Antillean landmass formed on the west of the Proto-Caribbean region during the late Lower Cretaceous. This landmass moved north-eastwards remaining close to the Yucatan Peninsula until the Eocene (Figs. 2, 3). During the Late Eocene–Oligocene this landmass was contiguous with Cuba and Puerto Rico before undergoing island–island vicariance (MacPhee & Iturralde-Vinent 1995). There is no evidence of island size change subsequent to this vicariance. During the mid-Tertiary the North and South American landmasses moved westwards relative to the Caribbean. During the period of amber-forming

resin secretion (15–20 million years ago; Iturralde-Vinent & MacPhee 1996) the Haitian part of Hispaniola lay directly south of and close to the south-eastern part of Cuba. Since then, the separation of the islands has continued until the far-western tip of Hispaniola was clear of the south-easternmost tip of Cuba (Fig. 4) (e.g., Ross & Scotese 1988). Spiders, in general, are renowned for their good dispersal capabilities and presumably did not require a land bridge in order to colonize Hispaniola. There are 291 Recent species in 155 genera and 40 families recorded from Hispaniola (Penney 1999), but this fauna has not been intensively investigated using a variety of collecting techniques (e.g., Banks 1903; Bryant 1943, 1945, 1948). The fossil fauna consists of approximately 200 species in 46 extant families (Penney 1999). Eleven of the families are recorded only from the fossil fauna and five are recorded only from the Recent fauna which is an overlap of approximately 70%. Coddington et al. (1991) suggested that one hectare of typical neotropical forest probably supported 300–800 different spider species, supporting the idea that the Recent Hispaniolan spider fauna is poorly known.

Species longevity.—Based on observations from the fossil record and/or Lyellian per-



Figures 1–4.—Palaeogeography of Central America and the Caribbean (after Ross & Scotese (1988)). 1, Early Aptian (118.7 Ma); 2, Middle Campanian (84.0 Ma); 3, Late Eocene (44.1 Ma); 4, Recent (0.0 Ma).

centages (the percentage of species in the fossil record that exist today), Stanley (1985) suggested a few million years for a number of groups of terrestrial animals, whereas plants and some marine animals were found to have longer species durations. Prószyński (1986), in a footnote, requested information regarding species longevity, and suggested that a salticid species may survive a few million years. Prószyński's estimate was speculative and based on the disjunct distributions of Recent species which were assumed to have been caused by the Pleistocene glacial and interglacial periods. He has no additional data that would more accurately estimate the species longevity for this family (J. Prószyński pers. comm. 1998). Decae (1986), however, suggested that two species of *Cyrtocarenum* Ausserer 1871 (Ctenizidae) may both have a minimum age of 23 million years. Decae (1986) only mentioned that 23 million years was the minimum age of the species in the abstract of his publication. Evidence was given for a possible

speciation event 23 million years ago resulting from vicariance (the separation of the Greek mainland into western and eastern parts divided by an oceanic trough).

Testing paleobiogeographic hypotheses.—With spiders, the analysis of Recent biogeographic patterns without evidence from the fossil record can be considered speculative at best. This is demonstrable by the numerous disjunct distributions between Recent spider families and genera and those preserved in the fossil record. Wunderlich (1994) discussed the biogeographic relationships of the extant and fossil central European spiders to the tropical and subtropical faunas. The families Archaeidae C.L. Koch & Berendt 1854, Deinopidae C.L. Koch 1851 and Cyatholipidae Simon 1894 (the fossils attributed to this family may be incorrectly placed; C. Griswold pers. comm.) were discussed with respect to their fossil (central Europe) and Recent (tropics and southern hemisphere) distributions. The presence of families and genera found in the fossil

record in central Europe, which today are only found in southern Europe, or are rare in central Europe, for example, Ctenizidae Thorell 1887, Dipluridae Simon 1889, Leptonetidae Simon 1890, Hersiliidae Thorell 1870, Oecobiidae Blackwall 1862 and *Orchestina* Simon 1882 (Oonopidae Templeton 1835) was reported by Wunderlich (1994).

Décade's (1986) logic does not consider the ancestral area(s) of the taxa or their ancestor(s). Three hypotheses for the Recent distributions of the Afrotropical genera of the family Archaeidae may be generated. Vicariance resulted from Madagascar separating from the African mainland. The following evolutionary events may have occurred: 1) the Madagascan genus *Archaea* C.L. Koch & Berendt 1854 may have evolved from a population of the south African (e.g., Dippenaar-Schoeman & Jocqué 1997) genus *Afrarchaea* Forster & Platnick 1984 (one species *A. godfreyi* (Hewitt 1919) is found in Madagascar (Lotz 1996), is not endemic, and has probably been introduced from South Africa); or 2) vice versa; or 3) both genera evolved from a common ancestor.

Madagascar separated from northern Gondwanaland and moved southwards to its present position over approximately 150 million years beginning prior to the Middle Jurassic initiation of sea-floor spreading in the Western Somali Basin (Coffin & Rabinowitz 1987). The presence of fossil evidence, i.e., the genus *Archaea* in Baltic amber (e.g., Eskov 1992) rejects two of these hypotheses as follows. Madagascar is renowned for its unique fauna and flora; it is unlikely that *Archaea* would colonize the Baltic region so far north without also crossing the relatively narrow Mozambique Channel to colonize the African mainland. The fossil evidence and Recent distribution suggests a much wider distribution of this genus in the past (e.g., Eskov & Golovatch 1986) probably prior to the separation of Madagascar from the mainland (the family is also recorded from the Jurassic of Kazakhstan (Eskov 1987)). Thus two of the above hypotheses (1 and 3) are rejected because both genera may have evolved from a common ancestor, but prior to the vicariance event in question. There is no evidence to support the remaining hypothesis that *Afrarchaea* evolved from *Archaea*; however, this hypothesis is subject to

falsification through the fossil record in the same manner as hypothesis 1.

Because fossils of Recent terrestrial animal species have not been found in rocks more than ten million years old, Eldredge (1985) proposed that all species alive more than about ten million years ago are extinct. All species described from Dominican Republic amber are extinct (with possibly a few exceptions, which warrant re-examination; e.g., Poinar 1992). Therefore a terrestrial invertebrate species longevity of less than 10 million years is a reasonable expectation. The obvious contraindication to this assumption are those Recent species considered to be 'living fossils', but these belong to extant clades known in the fossil record to show long and narrow clade shapes, i.e., occupying a long range of geological time and with few branches (Stanley 1985).

Hypotheses for the Hispaniolan spider fauna.—On the basis of the presence and absence data of spider families in the Dominican Republic amber, the Recent Hispaniolan spider fauna, and the Recent Neotropical spider fauna (Table 1—families known from all faunas and with both endemic and non-endemic Recent species not included) it is reasonable to expect that the families Cyrtachenidae Pocock 1903, Microstigmatidae Roewer 1942, Nemesiidae Simon 1892, Ochyroceratidae Fage 1912, Tetrablemmidae O.P.-Cambridge 1873, Palpimanidae Thorell 1870, Hersiliidae, Symphytognathidae *s.l.* Hickman 1931, Anapidae Simon 1895, Mysmenidae Simon 1922 and Hahnidae Bertkau 1878, have Recent representatives on Hispaniola which have yet to be discovered. These families are known from the Dominican Republic amber but not from the Recent Hispaniolan fauna, and are components of the Recent Neotropical fauna. Many of the smaller species (e.g., Ochyroceratidae, Tetrablemmidae, Symphytognathidae, Anapidae, Mysmenidae, Hahnidae), cryptic species (e.g., Cyrtachenidae, Microstigmatidae, Nemesiidae, Hersiliidae) or less common species (e.g., Palpimanidae) may have been overlooked in the early stages of a species inventory of Hispaniola, in favor of the larger and more common species. In the inventories listed by Bryant (1948) for Cuba, Puerto Rico, St. Vincent and the Virgin Islands the above families were represented only by the Hersiliidae recorded from Cuba,

Table 1.—Dominican Republic amber, Hispaniolan and Neotropical spider families considered in this paper, and the presence of Recent non-endemic and Recent endemic Hispaniolan species in those families.

Family	Dominican Republic (amber)	Recent Hispaniola		Recent Neo-tropical	Reference
		(endemic)	(non-endemic)		
Cyrtacheniidae	+	—	—	+	Wunderlich (1988)
Microstigmatidae	+	—	—	+	Wunderlich (1988)
Nemesiidae	+	—	—	+	Schawaller (1981)
Ochyroceratidae	+	—	—	+	Wunderlich (1988)
Tetrablemmidae	+	—	—	+	Wunderlich (1988)
Palpimanidae	+	—	—	+	Wunderlich (1988)
Hersiliidae	+	—	—	+	Wunderlich (1988)
Symphytognathidae <i>s.l.</i>	+	—	—	+	Schawaller (1981)
Anapidae	+	—	—	+	Wunderlich (1988)
Mysmenidae	+	—	—	+	Wunderlich (1998)
Hahniidae	+	—	—	+	New amber record
Filistatidae	—	—	+	+	Platnick (1993)
Desidae	—	—	+	+	Platnick (1993)
Deinopidae	—	—	+	+	Bryant (1948)
Drymusidae	—	+	—	+	Bryant (1948)
Amaurobiidae	—	+	+	+	Platnick (1997)
Scytodidae	+	—	+	+	Wunderlich (1988)
Oecobiidae	+	—	+	+	Wunderlich (1988)
Uloboridae	+	—	+	+	Wunderlich (1988)
Dictynidae	+	—	+	+	Wunderlich (1988)
Clubionidae	+	—	+	+	Wunderlich (1988)

and the Palpimanidae recorded from all but the Virgin Islands. Subsequently, Tetrablemmidae was recorded from Cuba and the Virgin Islands and Anapidae from St. Vincent (Platnick 1989); Palpimanidae from the Virgin Islands (Platnick 1993); Ochyroceratidae and Mysmenidae from Cuba and St. Vincent (Platnick 1997).

Endemic vs. non-endemic species.—Some, if not all, of the families known from the Recent, but not amber, Hispaniolan spider fauna (Table 1) may have colonized Hispaniola since the period of amber-forming resin production in the Tertiary. The only known Hispaniolan filistatid, *Kukulcania hibernalis* (Hentz 1842), is widespread on the American mainland and the only known desid on Hispaniola, *Paratheuma insulana* (Banks 1902), is found in America and the West Indies (Platnick 1993). The only Hispaniolan deinopid, *Deinopsis lamia* MacLeay 1839, is distributed throughout the Antilles; the only Hispaniolan drymusid, *Drymusia simoni* Bryant 1948, and two amaurobiids: *Tugana crassa* (Bryant 1948) and *Retiro gratus* (Bryant 1948) are endemic to Hispaniola. *Tugana cavatica* (Bryant

1940) is found on Cuba and Hispaniola (Alayón-García 1992).

It is possible that those families containing species endemic to Hispaniola (Drymusidae Simon 1893 and Amaurobiidae Thorell 1870) were present on Hispaniola at the time of the Dominican Republic amber formation although this cannot be established unequivocally unless they are found in the amber or other fossils from the region.

Assuming a species longevity of less than 10 million years, families with only non-endemic species on Hispaniola (discovered and undiscovered) must have colonized Hispaniola since the Tertiary amber-forming period or have colonized other regions from Hispaniola since the Tertiary. It is more likely that most of the families known from only non-endemic species also have undiscovered endemic species present, particularly those families present in Dominican Republic amber, as detailed below. The families Scytodidae Blackwall 1864, Oecobiidae, Uloboridae Thorell 1869, Dictynidae O.P.-Cambridge 1871, and Clubionidae Wagner 1887, are recorded in Dominican Republic amber; Filistatidae

Ausserer 1867, Deinopidae, and Desidae Pocock 1895, are not. Many Recent genera of Desidae live in the intertidal zones of rocky coasts and may have been present on Hispaniola during the Miocene but avoided capture in resin because of their habitat.

Eskov (1990) reported Filistatidae from the Upper Jurassic of Kazakhstan (but this material has yet to be published), before the formation of the Proto-Greater Antillean land mass. It is probable, then, that Filistatidae colonized Hispaniola from the American continent, possibly via Cuba. The same may be true for the Desidae, but the Recent distribution of the deinopid species (Greater Antilles) suggests a colonization event originating from within the Greater Antilles, possibly Hispaniola.

Families that have colonized Hispaniola, but which lack endemic species, have probably not been on Hispaniola long enough to speciate; these families must have colonized the island since the amber formation and within the last ten million years. Families represented in the Dominican Republic amber and known from the Recent fauna of Hispaniola from only non-endemic species (Table 1) may either have colonized other regions from Hispaniola, or have colonized Hispaniola from other regions.

Uloboridae and Dictynidae include species with distributions restricted to the Greater Antilles and these families may have colonized other regions from Hispaniola; the clubionid *Elaver exceptus* (L. Koch 1866) (possibly present on Hispaniola) is distributed from Canada, through the USA to the West Indies (Platnick 1993). On Hispaniola, Scytodidae is known only from pantropical species and, despite the lack of evidence, the probability of Hispaniola being scytodid ancestral area is unlikely due to the relatively young age and isolated nature of the island, and the cosmopolitan distribution of Scytodidae. On Hispaniola, Oecobiidae is known from one species *Oecobius concinnus* Simon 1892, collected from Port-au-Prince, Haiti; elsewhere in the region it has a distribution throughout the Caribbean islands, Peninsula Florida, coastal Mexico, Central America, Venezuela and Columbia (Shear 1970). Many oecobiids are synanthropic, small, often overlooked, and are frequently inadvertently transported by man. All of the records of this species given by Shear (1970)

are from coastal localities, so this was probably the means of dispersal for this species. Only 11 specimens are recorded from Hispaniola (Bryant 1948), compared with the hundreds of specimens collected from other regions, so this is probably an introduced species.

Families known from the Dominican Republic amber and recorded from the Recent Hispaniolan fauna from only non-endemic, presumably introduced species, unless their amber species lineages have become extinct since the Tertiary, might be expected to contain species endemic to Hispaniola that await discovery and description. The only known possible cause of major extinctions on Hispaniola since the amber formation might be the Pleistocene glaciations. Hispaniola lay in a tropical-subtropical zone with an arid glacial climate (in part, more arid than at present), and there is good evidence of a cooler Pleistocene climate from sedimentary and geomorphic data and alluvial terraces. However, extreme aridity and glaciation have not been documented for the Dominican Republic during the Pleistocene (Schubert 1988). Whilst the surrounding sea temperature dropped by approximately 2–3 °C during the glacial maxima (Prell et al. 1976), the albedo of Hispaniola was the same as it is at present (15–19%). The albedo increased during the last glacial maximum due to the expansion of savannah at the expense of tropical forest; e.g., Panama had a reflectivity of 15–19 percent during the last glacial maximum and at present has a reflectivity of 10–14% (Schubert 1988). Grimaldi (1996) presented a reconstruction of the Tertiary Dominican Republic amber-producing forest, based on fossil evidence, which differed little from a Recent Neotropical rainforest. It can be concluded that the Dominican Republic rainforest has suffered no drastic changes since the Tertiary that would cause the spider lineages present in the amber to become extinct.

Wunderlich (1988) recognized 25 Hispaniolan spider genera recorded only from fossil species. These genera may or may not be extinct. Considering the poorly known nature of the Recent Hispaniolan spider fauna, the lack of these genera in the Recent fauna cannot be construed as evidence for considering these genera extinct; they may contain extant species which have yet to be discovered.

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AN ADAPTIVE RADIATION OF HAWAIIAN THOMISIDAE: BIOGEOGRAPHIC AND GENETIC EVIDENCE

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ABSTRACT. The Hawaiian Thomisidae are noted for being extremely species rich, as well as diverse in morphology and ecology. This exceptional diversity led early systematists to place the species into several genera with cosmopolitan distributions. It has been recently suggested that these species compose a single large adaptive radiation. Species-area relationships for all thomisid species and for *Misumenops* F.O. Pickard-Cambridge 1900 (Thomisidae) species for various island areas were generated. Further, a phylogenetic hypothesis was constructed based on genetic distances between the Hawaiian thomisids and various outgroups using a 450 bp region of the mitochondrial cytochrome oxidase I (COI) gene to test for close genetic relationships. Despite the extraordinary isolation of the Hawaiian islands, the numbers of *Misumenops* and total thomisid species were found to be significantly higher than predicted for an island system of its size. Phylogenetic analysis of COI suggests the Hawaiian thomisids are more closely related to each other than to representatives of genera to which they have been previously assigned. These results support the existence of a Hawaiian thomisid adaptive radiation, and merit further investigation using comparative methods.

The biota of the Hawaiian archipelago is characterized by a number of large species radiations. These radiations result from the extreme geographic isolation and topographical diversity of the islands (Carson & Clague 1995). Natural colonization of the archipelago has been largely limited to organisms having exceptional dispersal capabilities, and those species that were successful colonizers experienced total genetic isolation from their source populations. Founders that made the long journey frequently underwent rapid evolution due to drift and selection in extremely small populations (Carson 1994). The Hawaiian Islands themselves are volcanic, formed at a "hot spot" connected to the Earth's core. As the Pacific tectonic plate continually rolls northwestward over the hot spot, new islands are formed. Consequently, they are arranged in chronological order. After initial colonization of the archipelago, it appears that taxa have frequently progressed down the island chain in a step-wise manner, resulting in repeated founder events as each new island is colonized (Wagner & Funk 1995). This unique combination of biogeographical events may explain some of the unusual aspects of the composition of the Hawaiian biota. For example, Hawaii's terrestrial biota is considered depauperate at higher taxonomic levels

due to its extreme isolation (Howarth & Mull 1992). However, the islands are exceptionally diverse at the species level, due to extensive autochthonous speciation. The diversity of Hawaiian spiders closely follows this pattern.

Of the 105 known spider families (Coddington & Levi 1991), only 10 occur naturally in the Hawaiian Islands, and many of these are represented by a single genus (Simon 1900; Suman 1964). Some of these genera have undergone extensive speciation (Gillespie *et al.* 1998). In particular, native species of the genera *Tetragnatha* Latreille 1831 (Tetragnathidae), *Argyrodes* Simon 1864 and *Theridon* Walckenaer 1805 (Therididae), *Misumenops* F.O. Pickard-Cambridge 1900 (Thomisidae), *Sandalodes* Keyserling 1883 (Salticidae) and *Cyclosa* Menge 1866 (Araneidae) are known to be unusually diverse and most, if not all, are endemic to the Hawaiian Islands (Table 1). It is likely that many more species within these groups remain to be discovered. However, because many species have extremely small ranges of endemism, rapid degradation of natural areas along with increasing numbers of alien species, make these spiders exceptionally vulnerable to extinction (Gillespie & Reimer 1993).

The family Thomisidae attracted attention early in the study of Hawaiian biology. R.C.L.

Table 1.—Species radiations of Hawaiian spiders.

Family	Genus	Native species	% Considered endemic		Reference
Tetragnathidae	<i>Tetragnatha</i>	>52	100		Gillespie <i>et al.</i> (1998)
Therididae	<i>Theridion</i>	>13	100		Simon (1900)
Therididae	<i>Argyrodes</i>	>30	100		Gillespie <i>et al.</i> (1998)
Thomisidae	<i>Misumenops</i>	17	100		Suman (1970)
Araenidae	<i>Cyclosa</i>	>7	100		Simon (1900)
Salticidae	<i>Sandalodes</i>	>9	88		Simon (1900)

Perkins, a pioneering Hawaiian naturalist and collector for the *Fauna Hawaiiensis* spent little time in the pursuit of spiders. However, he recognized that "the Thomisidae are probably the most interesting and important group in the Hawaiian spiders" (Perkins 1913). His collections were examined by Eugene Simon (1900), who described 14 new species and a new genus of Thomisidae. These 14 species were placed in the cosmopolitan genera *Misumena* Latreille 1804, *Diaea* Thorell 1869 and *Synaema* Fabricius 1775 as well as the new endemic genus *Mecaphesa* Simon 1900. In a subsequent revision of Hawaiian Thomisidae, Suman (1970) noted that the genitalia of the Hawaiian *Diaea* was extremely similar to that of the Hawaiian *Misumena* and these two genera were likely the same. Further, examination of the setation and eyes of Hawaiian spiders previously assigned to *Diaea* and *Misumena* revealed that they were actually more similar to representatives of *Misumenops*, a cosmopolitan genus, than to other representatives of *Diaea* and *Misumena*. Accordingly, representatives of *Diaea* and *Misumena* were placed in *Misumenops*. Suman considered the endemic *Mecaphesa* to be related to the genus *Ozyptila* Simon 1964, and further suggested that that all of the Hawaiian thomisids were likely derived from three separate colonizers, one that gave rise to the Hawaiian *Misumenops*, one that gave rise to the endemic genus *Mecaphesa*, and one that gave rise to the Hawaiian *Synaema* (Suman 1970). Suman's revision also resulted in the recognition of several new species, for a total of 21 described species, 17 of which are in the genus *Misumenops*.

Recently, Lehtinen (1993) has suggested that all Hawaiian thomisids comprise an adaptive radiation generated from a single founder,

one in which extensive adaptive morphological evolution has played a significant role. Examples of explosive adaptive radiations in island archipelagos illustrate how closely related species often display great morphological diversity (Grant & Grant 1989). This phenomenon is well documented in other Hawaiian spiders (Gillespie 1994; Gillespie *et al.* 1997), and other Hawaiian taxa (Roderick & Gillespie 1998). Consequently, if the Hawaiian thomisids constitute an adaptive radiation, they may represent another exceptional opportunity for understanding evolutionary and ecological mechanisms that generate rapid diversification.

In this study I examine the species richness of Hawaiian thomisids in a biogeographical framework. Classical biogeographical theory (MacArthur & Wilson 1967) states that island species diversity is a balance between immigration and extinction. What determines the rate of immigration and extinction depends largely on the size of an island and its distance from a source. In this context one would predict that the isolation and small size of Hawaii would result in a species poor fauna. Here I examine the species-area relationship for Hawaiian thomisids at the family and generic levels in comparison to other island areas. Also, I conduct a phylogenetic analysis of Hawaiian thomisid species and representatives of the genera to which they have been assigned historically, in order to provide corroborative evidence for a within-archipelago radiation.

METHODS

Biogeographical analysis.—A species-area curve was generated for both total thomisid species and for species in the genus *Misumenops*. Data for the distribution of thomisids and *Misumenops* species have been assessed in

Table 2.—Species used in sampling of a 450 bp region of mitochondrial cytochrome oxidase I.

Species	Collection locality
<i>Misumenops anguliventris</i> Simon 1900	Kauai, Oahu, Maui, Hawaii Island
<i>Misumenops cavatus</i> Suman 1970	Hawaii
<i>Misumenops discretus</i> Suman 1970	Kauai
<i>Misumenops editus</i> Suman 1970	Oahu
<i>Misumenops facundus</i> Suman 1970	Hawaii Island
<i>Misumenops insulanus</i> Keyserling 1890	Oahu
<i>Misumenops imbricatus</i> Suman 1970	Oahu, Maui
<i>Misumenops junctus</i> Suman 1970	Molokai
<i>Misumenops nigrofrenatus</i> Simon 1900	Kauai, Oahu, Hawaii Island
<i>Misumenops vitellinus</i> Simon 1900	Kauai, Oahu, Maui, Hawaii Island
<i>Mecaphesa perkinsi</i> Simon 1900	Oahu
<i>Mecaphesa semispinosa</i> Simon 1900	Oahu
<i>Synaema naevigerum</i> Simon 1900	Maui
<i>Synaema globulosum</i> Fabricius 1775	Mt. Carmel, Israel
<i>Xysticus</i> sp.	Westchester, New York
<i>Ozyptila georgiana</i> Keyserling 1880	Westchester, New York
<i>Misumena vatia</i> Thorell 1870	Maryland
<i>Misumenops asperatus</i> Hentz 1870	Maryland
<i>Misumenoides</i> sp.	Indiana
<i>Diaea</i> sp.	New Zealand

various island systems worldwide by a number of researchers: Andaman and Nicobar (Tikader 1977), Japan (Ono 1988), Britain and Ireland (Roberts 1985), Puerto Rico (Petrunkovitch 1930), Cuba (Bryant 1940), Tonga (Marples 1959), Fiji (Marples 1957), Pitcairn Islands (Benton & Lehtinen 1995), Philippines (Barrion & Litsinger 1995), Samoa (Marples 1957), Rapa (Berland 1924), Mauritius (Simon 18975), Galapagos Islands (Banks 1902), Tahiti (Berland 1934), and Marquesas Islands (Berland 1927). In the generation of the *Misumenops* species area curve, *Diaea* species from Tonga, Fiji and Samoa were substituted for *Misumenops*, as these were likely incorrectly diagnosed and are closely related to the Hawaiian thomisids (Suman 1970). Predictions of the total expected number of thomisid species and *Misumenops* species in Hawaii were calculated based on the species-area relationships generated.

Collection and identification of Hawaiian Thomisidae.—Hawaiian thomisid species were collected from native ecosystems on Kauai, Oahu, Maui, Molokai and Hawaii Island (Table 2). Specimens were collected by beating vegetation. Sexually mature spiders were identified to species using the Bishop Museum reference collection and Suman's (1970) key. Additional outgroup species were

collected from North America and Israel and others were kindly supplied by Dr. J. Robinson, Dr. G. Dodson, Cor Vink and Dr. W. Shipley.

Collection and analysis of genetic data.—DNA was extracted from the 13 Hawaiian species and 7 non-Hawaiian species listed in Table 2, using a phenol-chloroform preparation followed by ethanol precipitation (Palumbi *et al.* 1991). Voucher specimens were retained and will be deposited in the Bishop Museum, Honolulu, Hawaii. A 450 bp region of the mitochondrial gene cytochrome oxidase I (COI) was amplified for at least two individuals per species using a thermal cycler, with universal primers C1-J-1718 and C1-N-2191 (Simon *et al.* 1994). The COI gene was selected because it evolves rapidly in the third-codon position (Simon *et al.* 1994), providing sufficient variation to determine relationships between closely related species. This gene has been useful for assessing genetic diversity and phylogenetic relationships in other Hawaiian arthropods (Roderick & Gillespie 1998). PCR products were sequenced using an ABI 377 automatic sequencer and were aligned using Sequencher 3.0. Pairwise genetic distance (percent nucleotide difference between sequences) was calculated for all species using the Kimura 2-parameter correction

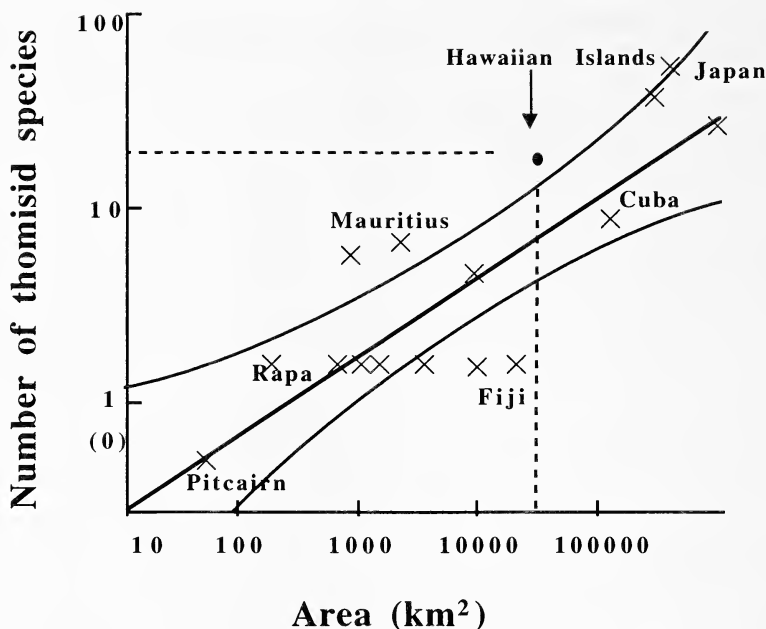


Figure 1.—Species-area relationship for total species in the family Thomisidae. Linear regression and a 95% CI on log-transformed data are shown. Equation of line is $\log(\text{species}) = 0.398 \log(\text{area}) - 0.917$, $R^2 = 0.70$, $P < 0.0001$. Expected number of species in the family Thomisidae is 7, while 21 species are observed.

for nucleotide bias (Kimura 1980), and a phylogenetic tree was constructed from these distances using a neighbor-joining algorithm in PAUP* 4.0 (Swofford 1998). The *Xysticus* sp. sequence was used to root the resulting tree.

RESULTS

Biogeographical analysis.—For the species-area in the family Thomisidae, a highly significant linear increase was found between the number of species and area of the island system (log-transformations, slope = 0.39, $R^2 = 0.70$, see Fig. 1). Perhaps not unexpectedly, Hawaii has an unusually high diversity for its size, falling just above the 95% confidence interval for the regression. The slope of the line indicates that an archipelago the area of Hawaii (28,314 sq. km), should have a total of 7 thomisid species, but 21 occur in Hawaii. The relationship for representatives of the genus *Misumenops* is quite different (Fig. 2). Whether or not Hawaii is included in the regression, there is no significant relationship between island size and number of *Misumenops* species ($R^2 = 0.49$, $P = 0.43$, for 15 islands not including Hawaii). By any measure, Hawaii appears to be an extreme outlier com-

pared to other island systems examined. For example, Hawaii has the highest observed diversity of *Misumenops* species (17), in contrast to the 1–4 species observed in other island systems. The number of *Misumenops* species on the 15 non-Hawaiian islands appeared to be normally distributed, and assuming normality, Hawaii falls far above the 99.999th percentile of the distribution. These results suggest that although thomisid diversity in the Hawaiian islands is high in general, *Misumenops* constitutes a disproportionate amount of this diversity. Further, the restriction of 17 of Hawaii's 21 thomisids to a single genus suggests that biodiversity in this island archipelago is a function of autochthonous speciation, rather than external colonization.

Analysis of genetic data.—Construction of a distance based phylogeny from 450 bp of COI revealed that the smallest genetic distances were found between Hawaiian thomisid species (Fig. 3). Thus the Hawaiian thomisids appear to be more closely related to each other than they are to representatives of *Misumena*, *Misumenoides*, *Diaea*, *Synaema*, and *Ozyptila*. The Hawaiian *Synaema* and non-Hawaiian *S.*

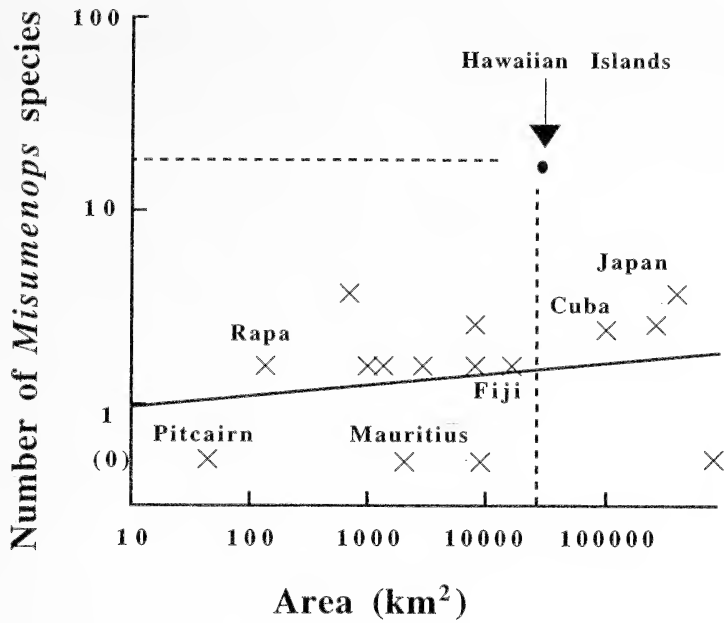


Figure 2.—Species-area relationship for species in the genus *Misumenops*, along with a simple linear regression on log-transformed data. Equation of line is $\log(\text{species}) = 0.054 \log(\text{area}) - 0.067$, $R^2 = 0.49$, $P = 0.43$. Expected number of Hawaiian species in the genus *Misumenops* is 0.6, while 17 species are observed.

globulosum are extremely distant while the Hawaiian *Synaema* is comparatively much more similar to the Hawaiian *Misumenops*, supporting Lehtinen's (1993) claim that the Hawaiian '*Synaema*' is not a true *Synaema*. Small genetic distances between non-Hawaiian *Misumenops asperatus* and all Hawaiian *Misumenops* species sampled suggests that the Hawaiian species are likely descended from a *Misumenops* ancestor. However, because *Misumenops asperatus* falls within the clade containing all Hawaiian thomisids, more than one colonization event is implied for the Hawaiian thomisid fauna. Sampling of many more *Misumenops* species from other geographic regions must be conducted in order to firmly establish what proportion of Hawaii's present day thomisid diversity has arisen through autochthonous species radiation.

DISCUSSION

The high diversity of *Misumenops* species in Hawaii, coupled with the short genetic distances between species, is a pattern similar to that found in other Hawaiian terrestrial arthropods that have undergone species radiation (Roderick & Gillespie 1998). While the islands are exceptionally diverse in both thom-

isid and *Misumenops* species, the *Misumenops* species represent nearly all of the thomisid diversity. It appears, therefore, that the number of successful colonizers is consistent with the island biogeography model. However, the model does not account for subsequent processes that occur over evolutionary time. Thus, despite few colonization events, autochthonous speciation raises the species diversity to levels higher than predicted by island area. Such a pattern might suggest that most of the available niche space for the family is being occupied by species in the genus *Misumenops*. Colonizing species may have undergone rapid ecological divergence in the absence of competition from other genera that exploit a variety of ecological strategies elsewhere.

Although Hawaiian *Misumenops* species are extremely diverse (Fig. 2), it is possible that this result may be biased by data points representing inaccurate estimates of diversity. Many of the data points used to generate the relationships between area and diversity were extracted from surveys of unequal sampling effort. Further, current revisions of these islands' spider fauna might result in different generic diagnosis of species. Consequently,

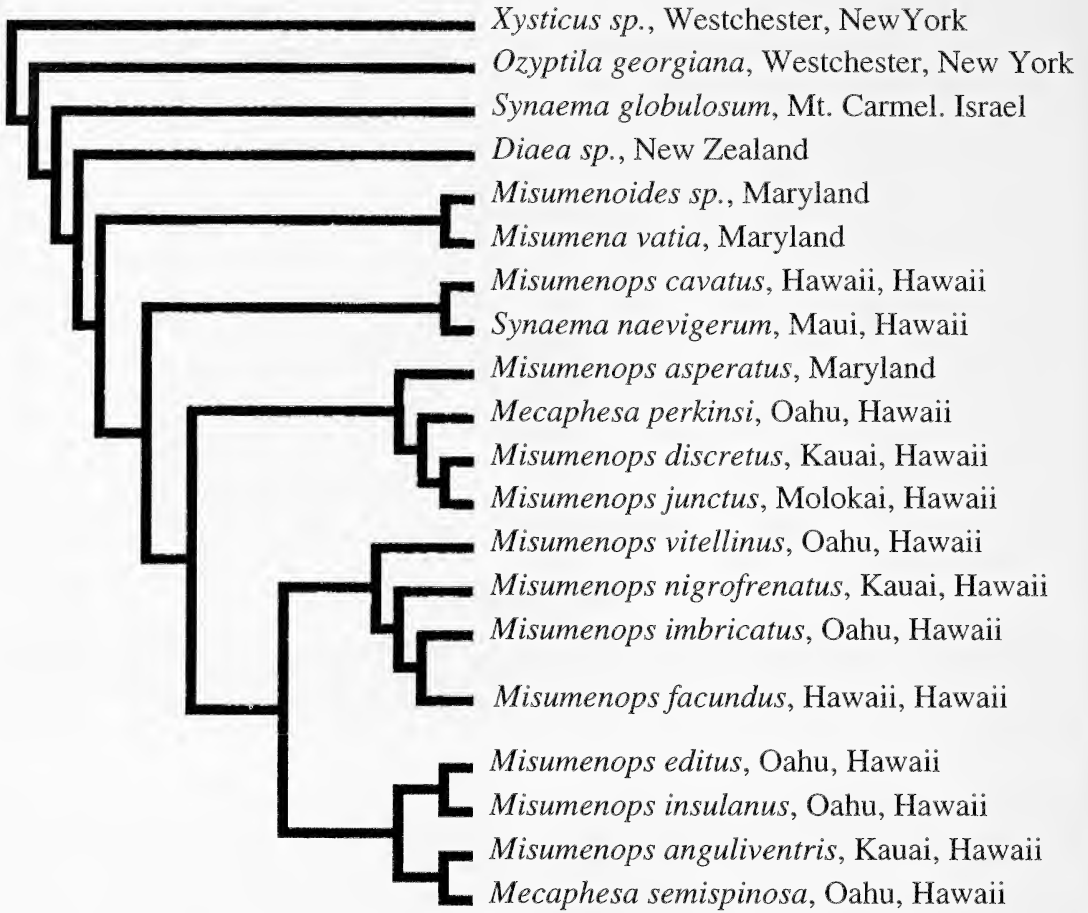


Figure 3.—A distance based phylogeny constructed from 450 bp of COI. Genetic distances were calculated using Kimura's (1980) 2-parameter corrected distance measure.

many of these points may represent over or under estimates of true diversity. It is possible that a more complete data set would reveal that Hawaii is not overly diverse in *Misumenops* or total thomisid species. However, Japan (the most thoroughly studied island group), has an area 10 times the size of Hawaii yet only twice the number of thomisid species (Ono 1988). Moreover, only three of these species are *Misumenops*. The relatively small genetic distances among Hawaiian species are consistent with the hypothesis that the high morphological and ecological diversity of Hawaiian thomisids is primarily the result of autochthonous radiation.

The Hawaiian *Misumenops* possess exceptional ecological diversity when compared to their continental congeners. Members of the family Thomisidae are well known for their employment of mimicry to ambush prey. The

tribe Misumenini Simon 1895, including spiders in the genera *Misumena*, *Misumenoides*, and *Misumenops* (Ono 1988), are commonly known as flower spiders because they mimic the coloration of flowers on which they sit in order to capture pollinating insects (Gertsch 1979). Recent research reveals that certain species of this tribe have ecological roles as nectivores and possible pollinators (Pollard *et al.* 1995). While genetic data suggest that the Hawaiian thomisids are descendants of flower spiders, Hawaiian thomisids are extremely diverse in their substrate affinities. For example, the green and brown speckled *Misumenops editus*, endemic to the summit of Mt. Kaala, Oahu, is perfectly camouflaged amongst its primary microhabitat of moss patches. Likewise, *M. aridus* and *M. nigrofrenatus* are well hidden on their substrate of white filamentous lichen. Other species are more specific to

green foliage. Many Hawaiian *Misumenops* that are ecologically separated as a result of differential substrate affinity are sympatric and may be very close relatives (Suman 1970).

In order to appreciate fully the extent of species radiation in the Hawaiian *Misumenops*, a complete phylogenetic construction is warranted. Only with a well-supported phylogenetic hypothesis can the idea of species radiation among the Hawaiian thomisids be tested rigorously. From such a hypothesis, one can determine the number of colonization events and the ecological diversity of this group. It is clear from data presented here that the Hawaiian *Misumenops* do not fit the classical model for island biogeography as they are species rich in an isolated and small island area.

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COMPARISON OF RATES OF SPECIATION IN WEB-BUILDING AND NON-WEB-BUILDING GROUPS WITHIN A HAWAIIAN SPIDER RADIATION

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ABSTRACT. The isolation of the Hawaiian archipelago has resulted in a fauna that shows high levels of endemism. I examined the role of lifestyle, as inferred from web-building versus non-web-building behavior, in dictating the rate of differentiation and species formation within a lineage of spiders in the genus *Tetragnatha* from the Hawaiian Islands. This genus comprises a group of morphologically, ecologically and behaviorally diverse taxa. Included in the radiation is a 'spiny-leg' clade which never builds webs and is relatively loosely associated with a specific habitat, and a large group of web-building species which are generally more tightly associated with a given substrate and habitat. Sequences of mitochondrial cytochrome oxidase DNA provided relative estimates of the age of a clade. Both linear and logarithmic models were used to estimate rates of speciation and the relative time required for speciation for each clade. The results showed that several small clades of web-building species have a greater rate of speciation as compared to the 'spiny-leg' clade. One explanation is that the web-building species may be capable of differentiation between more closely contiguous habitats, which would be consistent with the hypothesis that ecological differentiation promotes diversification and species formation. Possible alternative explanations for the results include differences in rates of molecular evolution, for example as a consequence of differences in metabolic activity.

The Hawaiian archipelago provides a natural laboratory for studies of speciation (Simon 1987). First, the extreme isolation of the islands has caused accentuation and acceleration of evolution in the archipelago, with numerous examples of rampant species proliferation (for reviews see Wagner & Funk 1995; Roderick & Gillespie 1998). Further, the islands are a series of volcanoes arranged within an identifiable chronological time frame (Carson & Clague 1995). The currently high islands range from Kauai, the oldest and most eroded, to Hawaii, the youngest, highest, and largest, with five separate volcanoes. Each volcanic mountain therefore shows a different stage in the evolutionary history of a clade, and allows determination of the nature of the relationship between evolutionary time and the abundance and distribution of a set of species. Radiations of spiders in the Hawaiian Islands include the genera *Tetragnatha* (as described below), *Argyrodes* (Simon 1900), *Theridion* (Simon 1900), and species in the family Thomisidae (Simon 1900; Suman 1970; J.E. Garb, this volume), among others (Gillespie et al. 1998).

I have been examining patterns of speciation (Gillespie 1991a, b, 1992a, Gillespie 1993; Gillespie & Croom 1995; Gillespie et al. 1994) and extinction (Gillespie 1992b, Gillespie & Reimer 1993) in a radiation of Hawaiian spiders in the long-jawed orb-weaving genus *Tetragnatha* (Tetragnathidae). Outside the archipelago, *Tetragnatha* is of worldwide distribution (Levi 1981), yet it is also one of the most homogeneous genera of spiders, in both morphology (elongate form [Kaston 1948]) and ecology (Caraco & Gillespie 1986; 1987a, b; Gillespie & Caraco 1987). Until 1991, information on the endemic Hawaiian tetragnathids was based on descriptions of only nine species (Karsch 1880; Simon 1900) in the genus *Tetragnatha* and one *Doryonychus*. Over the last 11 years I have collected native *Tetragnatha* in every native habitat type on all of the Hawaiian Islands. I have now described an additional 25 species of Hawaiian *Tetragnatha* (Gillespie 1991a, 1992a, 1994) and more than 60 additional new taxa have been collected, of which descriptions for many are near completion. The tetragnathid radiation spans a tremendous spectrum of col-

ors, shapes, sizes, ecological affinities, and behaviors (Gillespie 1991a, b; 1992a, b; 1994). Many species are web-building, with striking patterns, colors and structural modifications of the abdomen that allow concealment within specific microhabitats. Some species have structural modifications which appear to allow specialization on specific prey types. One entire clade ('spiny-leg' clade) has abandoned web building, with the concomitant development of long spines on the legs and adoption of a cursorial predatory strategy (Gillespie 1991a). This clade was originally described as 12 species. Recent molecular evidence indicates that an additional six species belong in this clade.

For the 'spiny-leg' clade I have generated hypotheses of evolutionary relationships among some species (Gillespie 1993; Gillespie & Croom 1995; Gillespie et al. 1994; Gillespie et al. 1997) and among populations within widespread species (Gillespie & Roderick unpubl. data.) based on molecular and morphological characters. I have also begun to study phylogenetic relationships among groups of web-building species, in which the component species are more sedentary and tend to be more tightly associated with a given habitat (Gillespie & Croom 1995; Gillespie et al. 1997).

Here, I quantify the relationship between the lifestyle of a clade and the rate of speciation. I focus on two monophyletic lineages, the 'spiny-leg' clade and a large web-building group, because of the contrast in vagility that their species display. The majority of the web-building species have become extreme habitat specialists, while the 'spiny-leg' species have abandoned web-building to become cursorial predators and tend to be less specific in habitat preference (Gillespie & Croom 1995). I use molecular sequence data to compare patterns of speciation among web-building and non-web-building lineages on different islands. I then examine relative rates of sequence divergence to determine the extent to which lifestyle (i.e., web-building or cursorial) is associated with the rate of speciation and relative time to species formation. Because the web-building species tend to be more tied to specific habitat types, the influence of disruptive selection may be enhanced relative to non-web-building species, and new species may

form more rapidly (Thoday 1972; Bush & Howard 1986).

METHODS

DNA sequences.—DNA sequence data have been generated based on part of the cytochrome oxidase subunit I (COI) mitochondrial DNA for almost all known representatives of Hawaiian *Tetragnatha*, and mitochondrial 12S ribosomal DNA sequences and allozyme data have been obtained for some representatives (Gillespie et al. 1997; R.G. Gillespie unpubl. data). For the current study I present molecular data from COI mitochondrial DNA only. A 450 base pair piece of COI was amplified for a minimum of two individuals of each species using primers C1-J-1718 and C1-N-2191 (designed by R. Harrison lab, Simon et al. 1994). Amplification was done with the following profile: 94 °C (60 sec), 48 °C (35 sec) and 72 °C (45 sec) for 40 cycles. Automated cycle sequencing was used to run and score the sequencing gels (ABI 377). Each sequence plot was inspected in Sequencher 3.1 (Gene Codes Corporation 1998). Alignments, which are straightforward for this protein-coding region, were performed by eye.

Species sampling.—The current study examines relative rates of speciation. Accordingly, I had to identify monophyletic clades, with all representatives included, prior to the analysis. For each of the clades chosen, the species group is recovered consistently by maximum parsimony and maximum likelihood analyses, and has bootstrap support of > 50% (most much higher; R.G. Gillespie unpubl. data). For the current study I obtained sequence data as follows: '*Spiny-leg*' clade: I obtained additional data from COI so as to have sequences for each of the following species, all of which have been described: *T. pilosa* Gillespie, *T. kauaiensis* Simon, *T. perreirai* Gillespie, *T. tantalus* Gillespie, *T. polychromata* Gillespie, *T. waikamoi* Gillespie, *T. brevignatha* Gillespie, *T. macracantha* Gillespie, *T. restricta* Simon, *T. kamakou* Gillespie and *T. quasimodo* Gillespie. Sequences were also obtained for an additional six representatives of the 'spiny-leg' clade which are undescribed. These 17 species encompass all known representatives of the 'spiny-leg' clade except for *T. mohihi* from Kauai, a small species that is known only from a single male (Gillespie 1991a).

Web-building species: I examined all known web-building species, most of which are undescribed. However, the analysis of speciation rates focused only on groups with > 50% bootstrap support (most much higher). One clade (54% bootstrap support) is from Maui and includes three described species: *T. stelarobusta* Gillespie, *T. trituberculata* Gillespie and *T. filiciphilia* Gillespie. A second clade (89% bootstrap support) is from Oahu, and includes four undescribed species which are readily identified on the basis of morphology (gross morphology and genitalic structure, Gillespie unpubl. data) and ecology: "Elongate Palikea" (Waianae Mountains, mid-elevation mesic forest), "Elongate Tantalus" (Koolau Mountains, mid-elevation mesic forest), "Slender Elongate" (Waianae Mountains, low elevation dry forest) and "Elongate Kaala" (Waianae Mountains, high elevation wet forest). A third clade (95% bootstrap support) is found on Kauai ("Elongate Kauai"), high elevation habitats on Maui ("Elongate Maui Crater") and Hawaii ("Elongate Mauna Kea"), and mid-elevation wet forest on Hawaii ("Elongate Hawaii Sadle").

Phylogenetic reconstruction.—Phylogenies were reconstructed using maximum likelihood as implemented in PHYLIP (Felsenstein 1993). This method can accommodate the heavy AT bias in the nucleotide composition (approximately 65% of the bases were A or T), using base frequencies estimated from the data. Maximum parsimony (PAUP* 4.0, Swofford 1998) was also used to test the robustness of the phylogenetic reconstruction. Transversions were weighted 4× transitions, roughly approximating the greater frequency of base changes that involved transitions (4×) between closely related species. Branches having maximum length zero were collapsed to yield polytomies.

Rates of speciation.—I used both linear and logarithmic models to estimate speciation rates as described by McCune (1998). Under the linear model, which assumes a "comb-shaped" tree, the rate of speciation (SR_{lin}) is calculated as:

$$SR_{lin} = n/t,$$

where n is the number of known species in a monophyletic clade and t is the age of the clade. The time required for speciation (TFS_{lin}) is:

$$TFS_{lin} = t/d = t/(n-1).$$

Under the logarithmic model, which assumes a symmetrical tree, the rate of speciation (SR_{ln}) is:

$$SR_{ln} = \ln n / \ln 2,$$

with the time required for speciation (TFS_{ln}) as:

$$TFS_{ln} = t/d = t \ln 2 / \ln n.$$

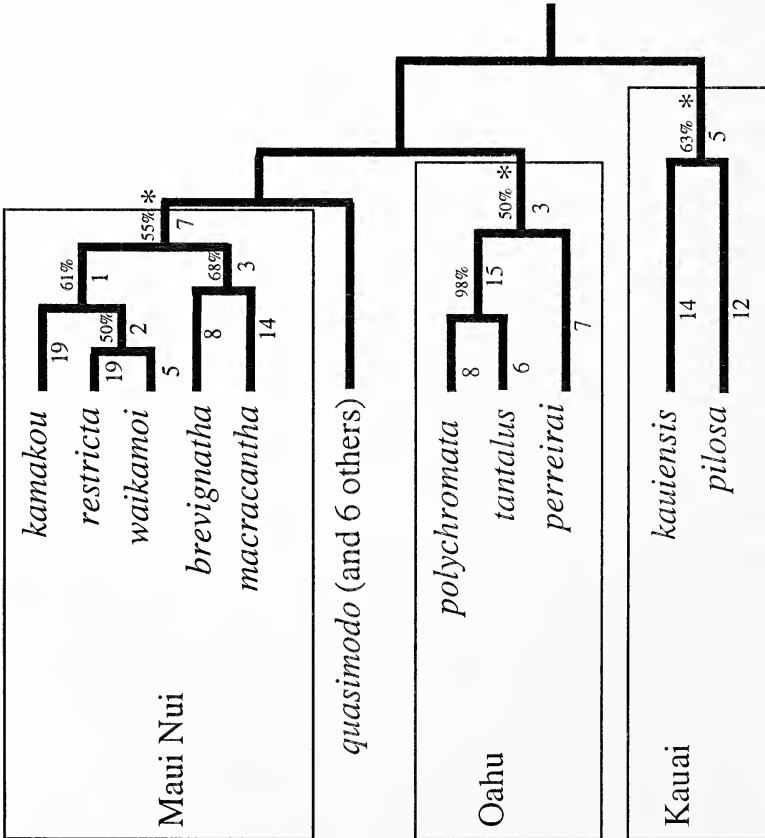
RESULTS

Molecular phylogenetic analysis.—For the range of genetic distances encompassing the major radiation of Hawaiian *Tetragnatha* both transitions and transversions increased linearly when plotted against Tamura distance (Tamura 1992) suggesting that both transitions and transversions are phylogenetically informative at this level and that the data, even at third positions, are not phylogenetically saturated (Gillespie et al. 1997). For the greater distances between the major Hawaiian radiation and species in the '*T. hawaiiensis*' clade (a separate introduction into Hawaii, Gillespie et al. 1994) transversions are still informative, although transitions show evidence of saturation. For the major radiation, sequences for the 450-base-pair homologous region were compared and variation was found at 204 different sites, with 111 being phylogenetically informative.

Phylogenetic relationships among representatives of the 'spiny-leg' clade of Hawaiian *Tetragnatha* based on COI sequences for each of the described species are shown in Fig. 1A. The relationships are similar to those described previously (Gillespie et al. 1997). The six recently described species all form a monophyletic group with *T. quasimodo*. However, because relationships between taxa in this clade were not resolved, these species are not included in the analysis of speciation. Relationships between species within the three selected web-building clades are shown in Fig. 1B.

Rates of speciation.—For each island group in the 'spiny-leg' clade, I summed the number of base changes from the base of the clade (marked * in Fig. 1A for each group) to the branch tip for each species in the clade. Then, for each clade, the average number of base changes for species within a clade was divided by the total number of bases to give the percent sequence divergence from the base of the clade to the present. An estimate of 2%

A. Spiny Leg Clade



B. Different Clades of Web-builders

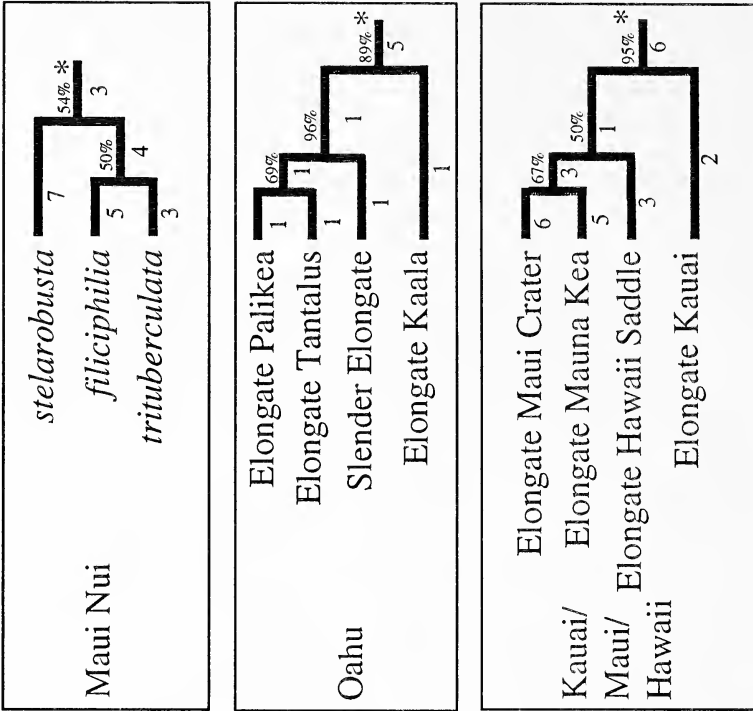


Figure 1.—Estimates of phylogeny for (A) representatives of the 'spiny-leg' clade of Hawaiian *Tetragnatha* (Gillespie et al. 1997) and (B) Different clades of web-building species. Numbers below branches indicate actual numbers of bases changes associated with that branch. * indicates the branch that was used as the "base" for each clade, and from which the numbers of base changes to the terminal nodes was counted.

Table 1.—Age of each clade, number of species, speciation rates, and times to speciation for: (A) the ‘spiny-leg’ clade, and (B) three different clades of web-building species, of Hawaiian *Tetragnatha*. * calculated assuming 2% sequence/10⁶ years (DeSalle et al. 1987). ¶ represents divergence from Oahu.

Island	A			B		
	Kauai	Oahu	Maui	Kauai– Hawaii	Oahu	Maui
Age (myrs)	5.1	3.7	1.9	5.1–0	3.7	1.9
Number of species	2	3	5	4	4	3
Av. % seq divergence	4.00	4.45	5.03	3.16	1.61	2.37
Age of clade (myrs)*	2.00¶	2.23	2.51	1.58	0.81	1.19
SRlin	1.00	1.35	1.99	2.54	4.97	2.53
TFSlin	2.00	1.11	0.63	0.53	0.27	0.59
SRln	0.35	0.49	0.64	0.88	1.72	0.93
TFSln	2.00	1.40	1.08	0.79	0.40	0.75

base change/10⁶ years was used to assess the age of a clade (DeSalle et al. 1987). This is an approximate measure, and is likely to deviate from the actual age of the clade because of the inconstancy of the molecular clock (J.H. Gillespie 1986). Accordingly, the age of the clade is used here as a relative measure only. Because the current study focuses on the comparison of two clades within the same genus in comparable habitats, base change differences between the two clades are likely to provide reliable relative estimates of differences in evolutionary rates. The age of each clade, the number of species, and both linear and logarithmic estimates of rates of speciation and relative times to speciation are given in Table 1A. Similar estimates were generated for the three clades of web-building species described above (Table 1B). Rates of speciation (both linear and logarithmic) were consistently higher for web-building species, and times to speciation were consistently lower for web-building species; these differences were all significant (Mann-Whitney *U*-test, *P* < 0.05).

DISCUSSION

The results show that the patterns of speciation relative to island age are similar in both ‘spiny-leg’ and web-building species groups: In both cases, speciation appears to have occurred largely within an island (Gillespie et al. 1997). However, the rate of species formation for the web-building clades contrasts with that of the ‘spiny-leg’ clade. In particular, differentiation between taxa within each of the web-building clades appears to oc-

cur much more rapidly. The higher rate of species formation in this clade may arise partly from their web-building habit. Based on current theories, groups that are only loosely associated with habitat types, such as the Hawaiian *Drosophila* and the cursorial ‘spiny-leg’ clade of Hawaiian *Tetragnatha*, may require longer periods of isolation in order to initiate divergence (Mayr 1963; Carson 1986; Bush & Howard 1986). However, groups comprising taxa with more rigorous ecological associations could diverge more rapidly between contiguous habitats through the action of forces such as disruptive selection (Rausher 1984; Rosenzweig 1990). Spiders that build webs tend to demonstrate stronger habitat affinities than cursorial species (Gillespie & Croom 1995), and consequently may be capable of differentiating more rapidly.

There are alternative explanations that might account for the differences in relative rates of species formation between the ‘spiny-leg’ and web-building species. In particular, both metabolic rate and generation time are known to affect rates of molecular evolution (Martin & Palumbi 1993): Higher metabolic rate and shorter generation time cause acceleration of molecular evolution. Although we have no evidence to suggest differences in generation time between the ‘spiny-leg’ and web-building species, it may be that the metabolic rate is higher among representatives of the more active ‘spiny-leg’ clade.

The age of the islands can be compared with estimates of the ages of the different clades based on sequence divergence for the

'spiny-leg' clade, assuming a constant substitution rate of 2% per million years (DeSalle et al. 1987; Juan et al. 1996) (Table 1A). The Kauai and Oahu clades might be expected to match the age of Oahu (3.7 myrs), as the formation of this island would have allowed divergence to be initiated. However, these two clades are considerably younger (2.0 and 2.2 myrs), suggesting perhaps that colonization and divergence started well after the formation of Oahu, or that molecular evolution is more rapid than that of other arthropod taxa for which calibrations have been made. On the other hand, divergence of the Maui species in the 'spiny-leg' clade are considerably older than the oldest of the islands in the Maui Nui complex (Molokai, Maui, Lanai and Kahoolawe). This result suggests that divergence of the Maui 'spiny-leg' clade was initiated prior to the colonization of Maui. Alternatively, rates of evolution may vary more than expected, and provide only very poor estimates of the age of a clade (J.H. Gillespie 1986; Kambhampati & Rai 1991). Within a lineage, acceleration in rates of sequence divergence may be associated with the formation of new species (Carson & Templeton 1984). Accordingly, the greater apparent age of the Maui species may be merely a reflection of the greater number of species.

Whether or not the DNA sequences provide an indication of actual age of a clade does not affect the major conclusions of this study. Here, the estimates of sequence divergence are used as a relative measure only, to compare groups of spiders that differ in lifestyle (web-building or non-web-building). The results suggest that there are much smaller genetic distances involved in species formation in web-building as compared to non-web-building species of Hawaiian *Tetragnatha*. It appears, therefore, that lifestyle, as indicated by the web-building habit, dictates in part the rate at which differentiation and divergence can occur within a lineage.

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FOSSIL EVIDENCE, TERRESTRIALIZATION AND ARACHNID PHYLOGENY

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ABSTRACT. Geological and morphological evidence suggests that the earliest scorpions were at least partially aquatic and that terrestrialization occurred within the scorpion clade. Scorpions and one or more other arachnid lineages are therefore likely to have come onto land independently. The phylogenetic position of scorpions remains controversial and we question Dromopoda, in which scorpions are placed derived within Arachnida, as this is not supported by scorpions' lateral eye rhabdomes, embryology and sperm morphology. We propose a synapomorphy for scorpions + eurypterids, a postabdomen of five segments as part of an opisthosoma of 13 segments. Scorpions and tetrapulmonates must have evolved their book lungs convergently while fossil evidence indicates that a stomotheca, synapomorphic for Dromopoda, is probably convergent too. 'Arachnid' characters such as Malpighian tubules, the absence of a carapace pleural margin, and an anteriorly directed mouth may also be convergent, although their status as synapomorphies can be defended using parsimony. Convergence is difficult to prove unequivocally, but when there are strong grounds for suspecting it, such characters are questionable evidence for arachnid monophyly.

Living arachnids are predominantly terrestrial, with those groups found in aquatic habitats, such as the water spider *Argyroneta* or halacaroid mites, assumed to have returned to the water secondarily. It is also reasonable to assume that the earliest chelicerates were aquatic, including the ancestors of arachnids (e.g., Kraus 1976). Terrestrialization was a key event in arachnid evolution and as there is good evidence for aquatic fossil scorpions (Jeram 1998), terrestrialization probably occurred independently within at least two arachnid lineages. The position of the scorpions within Chelicerata has proved to be controversial (e.g., Weygoldt 1998) and we do not accept that scorpions are a derived group within arachnids, nor that Arachnida is monophyletic. A number of characters which have been used to support arachnid monophyly could also be interpreted as adaptations for life on land (e.g., Kraus 1976). We consider these to include book lungs, Malpighian tubules, absence of carapace pleural margin, and an anteriorly directed mouth. Parsimony analyses (e.g., Wheeler & Hayashi 1998) suggest that these characters should be treated as homologous and apomorphic. However, if at

least two arachnid lineages moved onto land independently it would be surprising to find terrestrial adaptations in the common ancestor of all arachnids, irrespective of whether or not they were monophyletic, as this was an aquatic animal. These arguments are expanded below.

THE AQUATIC NATURE OF PRIMITIVE SCORPIONS

A number of authors have suggested that some of the oldest fossil scorpions were partially or wholly aquatic (e.g., Pocock 1901; Kjellesvig-Waering 1986). This proposal has not gone unquestioned. Petrunkevitch (1953) found no evidence for scorpion gills and argued that all other arachnids have book lungs or tracheae. More recently Weygoldt & Paulus (1979) again questioned whether scorpions really were aquatic, with Weygoldt (1998) finding Kjellesvig-Waering's (1986) evidence for scorpion gills unconvincing. Størmer (1970) and Brauckmann (1987) also described scorpion gills, although these structures projecting beyond the body margin are equivocal as respiratory organs and do not resemble xiphosuran book gills. Gills in scorpions have not,

therefore, been proven, but in his recent phylogeny of Silurian and Devonian scorpions Jeram (1998) presented both sedimentological and morphological evidence that at least some of these early scorpions were aquatic. His most basal scorpion taxon comes from the Devonian Hunsrückschiefer, a fully marine sequence (Bartels *et al.* 1998), while other Silurian taxa come from marginal marine deposits. Morphological evidence for an aquatic habitat includes the presence of gnathobases in some taxa, lack of an oral tube for liquid feeding, single-clawed, digitigrade tarsi, and abdominal plates lacking book lung spiracles. Jeram (1998) further commented that two or more scorpion lineages might have come onto land independently, but that this would be difficult to detect as many of the characters he analyzed were likely to have altered state during terrestrialization.

Scorpions have obvious autapomorphies (pectines, sting, pedipalpal claws) and there is no evidence to derive any other arachnid order directly from the scorpion clade, e.g., Anderson (1973); something which would require autapomorphy reversal. It is conceivable that scorpions and other arachnids evolved on land from a common terrestrial ancestor and that some scorpions then re-entered the water and lost their terrestrial adaptations. However, as the fossil record shows an accumulation of terrestrial-related features through the Palaeozoic (e.g., Selden & Jeram 1989, fig. 4), this remains an unlikely scenario. We therefore suggest that if the oldest scorpions were aquatic (Jeram 1998), they must have diverged from the other arachnids while still in the water and moved onto land independently.

SCORPIONES + EURYPYTERIDA

The phylogenetic position of scorpions remains controversial with the three principal cladistic analyses (Weygoldt & Paulus 1979; Shultz 1990; Wheeler & Hayashi 1998) including them in a monophyletic Arachnida, although differing in placement of the order. Weygoldt & Paulus (1979) and Weygoldt (1998) placed scorpions as a sister group to all other arachnids. However, the analyses of Shultz (1990) and Wheeler & Hayashi (1998) (primarily using Shultz's morphological data) placed scorpions higher in the Arachnida as a sister group to Haplocnemata (Pseudoscorpiones + Solifugae) with Opiliones as sister

group to all three, forming the taxon Dromopoda. Several authors have suggested that scorpions are most closely related to eurypterids (e.g., Versluys & Demoll 1920; Bristowe 1971; Kjellesvig-Waering 1986). These studies generally relied on overall similarities rather than discrete synapomorphies, and were justifiably criticized for this by Shultz (1990). While Shultz (1990) found scorpions to be derived arachnids, he excluded from his analysis Weygoldt & Paulus' (1979) character 21 (star-shaped lateral eye rhabdomes in scorpions and xiphosurans, quadratic in all other arachnids bearing lateral eyes). Wheeler & Hayashi (1998) did include this character. Both Wheeler & Hayashi (1998) and Shultz ignored Anderson's (1973) observation that the embryological development of scorpions and xiphosurans is similar in possession of a growth zone giving rise to both the prosoma and opisthosoma, while in all other arachnids this growth zone gives rise to the opisthosoma only. The distribution of these characters does not favor placement of scorpions as derived arachnids with Xiphosura as an outgroup. Furthermore, the analysis of Shultz (1990) found spermatozoa with a coiled flagellum axoneme to be synapomorphic in Arachnida, despite retention of a free flagellum in scorpion spermatozoa (the presumed plesiomorphic state). Weygoldt & Paulus (1979) proposed a coiled flagellum as synapomorphic only for non-scorpion arachnids. Alternatively, the eye rhabdome, growth zone character and sperm flagellum could all be reversals in the scorpion clade.

Dunlop (1998) stated that the clearest potential synapomorphy for scorpions and eurypterids is the five-segmented postabdomen, an obvious character (Fig. 1) ignored by cladistic studies. Shultz (1990) and Weygoldt (1998) argued that similarities between eurypterids and scorpions were probably symplesiomorphic, as they occurred in xiphosurans, too. Outgroup comparison with trilobites and other arachnates indicates that lack of a postabdomen is the plesiomorphic state with respect to Chelicerata, while in synziphosurines (primitive xiphosurans; Anderson & Selden 1997) and some arachnids there is a postabdomen of three segments (the pygidium of Shultz 1990). In support of the homology of the postabdomen we argue that scorpions and eurypterids have a groundplan of 13 opistho-

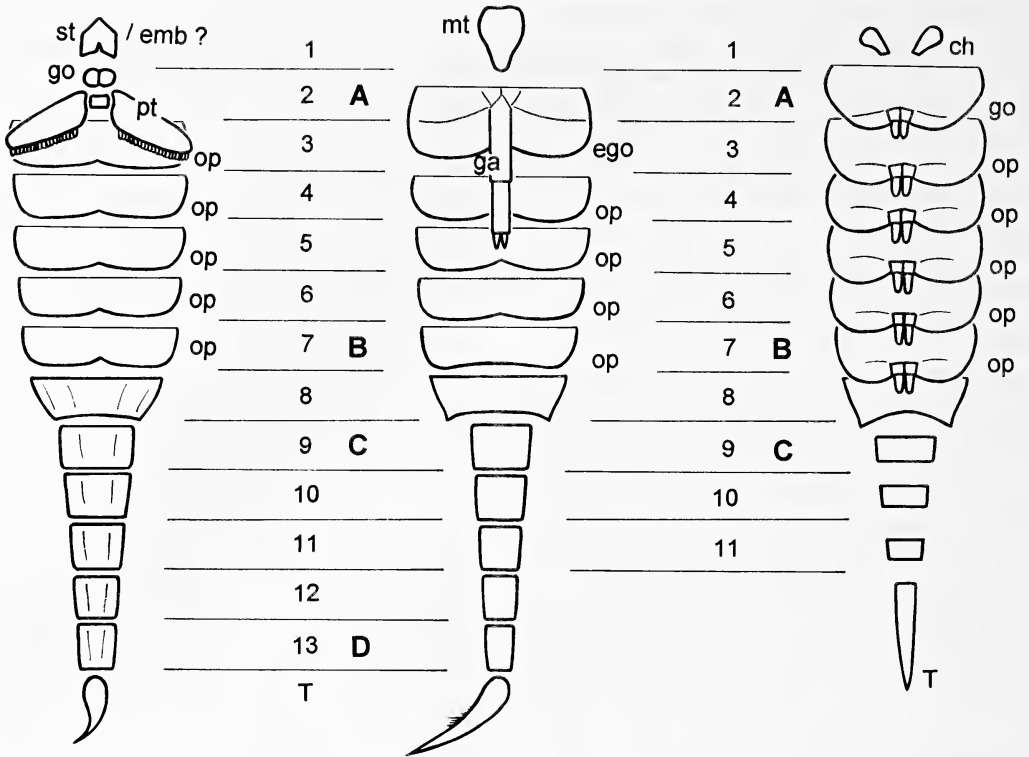


Figure 1.—Proposed homology of the ventral opisthosoma of a Paleozoic scorpion (left) a scorpion-like eurypterid (center) and a synziphosurine (right). This model differs in its placement of the pectines from Dunlop (1998, fig. 4) and it should be added that the chilaria in at least some synziphosurines may have been fully pediform (L. Anderson pers. comm.). Our model lines up four morphological reference points: the genital segment (A), the last opisthosomal appendage pair (B), the first postabdominal segment (C) and the posteriormost, 13th segment (D). Points A–C, i.e., the preabdomen, are seen in Scorpiones, Eurypterida and Xiphosura; C–D, i.e., the 5-segmented postabdomen, is synapomorphic for Scorpiones + Eurypterida. Opisthosomal segments numbered. Abbreviations: T = telson, st = sternum, emb = embryonic appendages, mt = metastoma, go = genital operculum, ego = eurypterid genital operculum formed from two fused appendage pairs, pt = pectines, ga = genital appendage, ch = chilaria, op = appendage-derived operculum, a structure usually termed Blatfuss (literally ‘sheet foot’) in eurypterids.

somal segments: A preabdomen (segments 1–8) and a postabdomen (segments 9–13).

THE QUESTION OF OPISTHOSOMAL SEGMENTATION

In scorpions.—The groundplan of arachnids has widely been quoted as comprising an opisthosoma of 12 segments (e.g., Kraus 1976; Shultz 1990). However, there is evidence for a transitory pair of pregenital limb buds described in scorpion embryos (Brauer 1895) representing an ‘extra’ segment, the nerve ganglion of which is retained (Anderson 1973). A scorpion with 13 segments, including this embryonic one, was figured by Millot (1949, figs. 52, 53). Shultz (1990) coded scorpions as lacking appendages on opisthosomal

segment 1 despite evidence for their presence embryologically in the less derived, apoikogenic scorpions (Anderson 1973). Scorpion opisthosomal segmentation has therefore been proposed as: (1) embryonic, (2) genital opercula, (3) pectines, (4–7) book-lungs, (8) last preabdominal segment and (9–13) postabdomen, plus a telson (e.g., Dunlop 1998).

In some of the earliest scorpions there is an additional abdominal plate (Jeram 1998) apparently representing an additional segment. While modern scorpions have four appendage-derived book lungs on the preabdomen, some early derivative scorpions have five appendage-derived opercula (Fig. 1) posterior to the genital operculae and the pectines. This could be interpreted as evidence that scori-

ons have a groundplan of 14 opisthosomal segments, e.g., (1) embryonic, (2) genital opercula (3) pectines, (4–8) book-lungs, (9) last preabdominal segment and (10–14) postabdomen, plus a telson. However, all known fossil and Recent scorpions express only 12 tergites, the last five of which are fused with the sternites into the postabdomen (Fig. 1). It should be possible to match all tergal and sternal elements.

Weygoldt & Paulus (1979, fig. 2) accepted that there are 13 ventrally expressed structures in Recent scorpions, but cautioned that there is no musculature evidence for an additional tergal element; i.e., they interpreted scorpions as having only 12 segments. They suggested that the 'extra' segment in scorpions is the result of the division of the ventral elements of opisthosomal segment 2; for them a scorpion autapomorphy. Essentially they argued that both the genitalia and pectines belonged to opisthosomal segment 2, a proposal which we support (Fig. 1). However, these authors were not aware of the additional abdominal plate in fossil scorpions, a fully expressed structure which appears to bring us back to a body plan of 13 opisthosomal segments: (1) embryonic, (2) genital opercula + pectines, (3–7) abdominal plates, (8) last preabdominal segment, (9–13) postabdomen, plus a telson (Fig. 1).

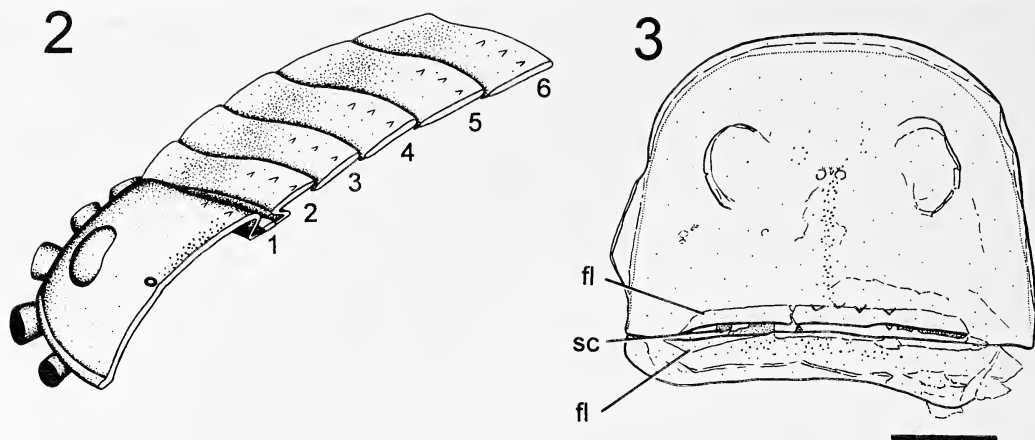
Our model is tentative, but we believe it fits the available data and means that, like xiphosurans, the scorpion groundplan consists of eight preabdominal segments with appendages on segments 1–7 (Fig. 1). We are still 'missing' a tergite in scorpions, but the first tergite in chelicerates is often reduced and has been overlooked in eurypterids (below). This model requires loss of one abdominal plate in more derived scorpion clades. This is reflected in the cladogram of Jeram (1998, fig. 2, node F).

In eurypterids.—Eurypterids are typically reconstructed with 12 opisthosomal segments. However, Raw (1957) cited evidence found by Holm (1898, pp. 8–9, fig. 15) for an 'extra' segment in eurypterids, a proposal overlooked by recent authors. Raw (1957, pp. 160–161, fig. 8c) proposed that the membranous fold between the carapace and the opisthosoma formed a discrete but highly reduced segment in eurypterids. Raw (1957) argued that what was traditionally interpreted as the first tergite

of eurypterids does not tuck under the posterior margin of the carapace, as the tergite does in xiphosurans. Instead, the membrane behind the eurypterid carapace is reflexed forward and then doubles back on itself in a manner consistent with it being a reduced and poorly sclerotized tergite (Fig. 2). One of Holm's eurypterid preparations (British Museum Natural History specimen I. 3406 (6)) was examined and shows these reflexed membranes (Fig. 3). What has traditionally been called tergite 1 in eurypterids is in contact with the carapace at its lateral margins, but has a slightly concave anterior margin forming a narrow gap on the midline in which there is a membrane containing thin fragments of sclerotized cuticle (Fig. 3). This, we believe, is consistent with it being a highly reduced tergite; our tergite 1.

Reduced first opisthosomal tergites are common in chelicerates as shown by xiphosuran microtergites (Anderson & Selden 1997) and the pedicels of some arachnids (Shultz 1990). These eurypterid cuticle fragments could be dismissed as having simply sutured off from the carapace or adjacent tergite, and we have noted Weygoldt & Paulus' (1979) evidence against an extra tergite in scorpions above. However, eurypterid ventral anatomy can also be homologized with our scorpion model (Fig. 1). The eurypterid metastoma is interpreted as opisthosomal segment 1, though it is unclear whether it is a sternal or appendicular structure. Jeram (1998) suggested that what is traditionally called the scorpion sternum is homologous with the eurypterid metastoma, and as such both may be appendage-derived elements, homologous with xiphosuran chilaria (Fig. 1). It is conceivable that the embryonic limb buds in scorpions actually become the scorpion sternum. Both are in approximately the same position and the fate of the limb buds and origins of the sternum are equivocal. This limb bud/sternum question merits investigation. Assuming homology (segment 1), the next segment in both scorpions and eurypterids bears the gonopore (segment 2). This fits the general chelicerate pattern of a gonopore on opisthosomal segment 2, which appears to be a valuable marker for homologizing segments (e.g., Millot 1949).

The eurypterid gonopore on opisthosomal segment 2 lies at the base of the genital appendage. The appendage is part of the large



Figures 2–3.—Eurypterid dorsal segmentation. 2. Schematic adaptation of Holm's (1898) observation that the dorsal membrane between the prosoma and opisthosoma in eurypterids folds back on itself. This differs from the way that the other tergites connect to each other. Raw (1957, fig. 8C) cited this as evidence that this membrane represents a highly reduced first opisthosomal tergite giving eurypterids 13, not 12, opisthosomal segments; 3. Camera lucida drawing of BMNH I. 3406 (6) a small, translucent specimen of *Baltoeurypterus* acid-etched from the matrix. This specimen supports Raw's interpretation by showing the folding of the membranes at the prosoma-opisthosoma junction (fl) and the slight sclerotization within this membrane (sc), which we interpret as opisthosomal tergite 1. Scale = 5 mm.

genital operculum which is divided by a transverse suture, suggesting it is formed from the fused appendages of segments 2 and 3. That scorpion pectines possibly belong to the genital segment is interesting in this context. Simon Braddy (pers. comm.) suggested that the paired pectines of scorpions could be homologous with the paired furcae at the end of the eurypterid genital appendage; a structure which also appears to belong to opisthosomal segment 2 (see also Braddy & Dunlop 1997).

In eurypterids, segments 3–7 bear gill tracts (probably non-homologous with book gills [Manning & Dunlop 1995]), and the last preabdominal segment is segment 8. There is a five-segmented postabdomen (segments 9–13) plus a telson (Fig. 1). This segmentation pattern merits further investigation. Our model (Fig. 1) suggests homology of several reference points: The genital segment (A), the posteriormost opisthosomal appendages (B), the start of the postabdomen (C), and the five segments to the 13th, posteriormost segment (D). Points A, B and C also match the body plan of xiphosurans (Fig. 1). Scorpions, eurypterids, and xiphosurans share an 8-segmented preabdomen with appendages on segments 1–7, while scorpions + eurypterids show an apomorphic 5-segmented postabdo-

men. No other chelicerates show an 8-segmented preabdomen.

Thirteen opisthosomal segments could be interpreted as a synapomorphy for Scorpiones + Eurypterida, though in reality this and the postabdomen are probably best treated as expressions of the same character. We have argued that the postabdominal segments (9–13) are homologous in these taxa and that the character state is derived. No outgroup shows a 5-segmented postabdomen. The three-segmented postabdomen of some arachnids (Shultz 1990) is unlikely to be derived from this condition by loss of two segments, as this would reduce the total number of opisthosomal segments to only 11 (arachnids such as thelyphonids have 12 segments).

PROBABLE CONVERGENT CHARACTERS

We have proposed one morphological synapomorphy shared by scorpions and eurypterids. Other characters have been used to support a monophyletic Arachnida and/or a derived position for scorpions within arachnids. Some of these characters appear to be adaptations for, or associated with, life on land. If arachnids terrestrialized more than once, then terrestrial adaptations are likely to

be convergent. It would be surprising to find terrestrial characters in the aquatic common ancestor predicted by arachnid monophyly and the models of Weygoldt & Paulus (1979), Shultz (1990) and Wheeler & Hayashi (1998).

Book lungs.—Book lungs are a 'textbook' arachnid character. However, their distribution indicates that although book lungs in scorpions and other arachnids are clearly homologous with respect to the pre-existing abdominal appendages, the book lungs of scorpions are not directly homologous with those of tetrapulmonates (contra Wheeler & Hayashi 1998). Weygoldt (1998) and Dunlop (1998) independently noted that only tetrapulmonate arachnids retain a respiratory organ on the genital segment. It is absent in xiphosurans, scorpions and probably eurypterids. Weygoldt (1998) regarded loss of a respiratory organ on the genital segment as most likely being convergent. Dunlop (1998) noted that outgroups such as trilobites have a respiratory organ on all opisthosomal segments, and proposed that the most parsimonious interpretation of this character is to treat it as plesiomorphically retained in tetrapulmonates and synapomorphically lost in a xiphosuran, scorpion and eurypterid clade.

In either case, book lungs in spiders and scorpions are not directly homologous, belonging to opisthosomal segments 2–3 in tetrapulmonates and 4–7 in scorpions (Dunlop 1998; Kraus 1998). Probable independent terrestrialization of scorpions and other arachnids indicates that their book lungs evolved independently from gills in response to the demands of breathing on land. Differences in detailed lung anatomy might be predicted between scorpions and other arachnids. This represents an interesting line of research which could be applied to other morphological structures which may be terrestrial adaptations, e.g., trichobothria, and details of limb morphology and mouthpart structure.

Stomotheca.—Shultz's (1990) taxon Dromopoda is supported by a number of appendicular characters coded primarily from Recent terrestrial forms. The strongest appears to be presence of extensor muscles, but specializations of the femorpatellar and patello-tibial leg articulations, and a stomotheca formed from coxal endites are included. The stomotheca creates a preoral cavity where extraintestinal digestion takes place. This feed-

ing process is less likely (although possible) in an aquatic animal. Weygoldt (1998) rejected Dromopoda, arguing that a stomotheca is clearly absent in many fossil scorpions (see also Jeram 1998, character 23), in solifuges, and in pseudoscorpions. Weygoldt (1998) concluded that either the stomotheca is convergent (supported here) or that scorpions must be paraphyletic. This example illustrates the dangers of ignoring fossil data when coding characters.

Malpighian tubules.—Malpighian tubules are endodermal extensions of the gut found in most arachnids, but not in palpigrades, opilionids and pseudoscorpions (Shultz 1990). They also occur convergently in insects. Their function is to remove excretory products such as guanine and uric acid from the body (e.g., Seitz 1987). They are not present in xiphosurans and their presence or absence is unknown in eurypterids. The tubules could be convergent terrestrial adaptations for removing dry, low-toxicity excretory products (e.g., guanine), given the importance of water conservation for animals on land (Kraus 1976).

Poorly developed carapace pleural margin.—The carapaces of xiphosurans, and to a lesser extent eurypterids, project laterally and form a cavity around the coxosternal region (Shultz 1990). This projection is not seen in arachnids. Its association primarily with taxa that masticate food using gnathobases may be significant; it is also seen in outgroups such as trilobites, although it is not apparent in fossil or Recent scorpions. Shuster (1950) noted that xiphosurans feed by burying themselves into the substrate in pursuit of worms and mollusks. The carapace pleural margin, and the associated cavity it creates, forms a semi-enclosed chamber within the substrate in which the gnathobases are free to masticate food. With a move towards terrestrialization and away from feeding in the substrate, a carapace pleural margin could become non-functional and lost. In contrast, many arachnids show a trend towards developing a preoral cavity (e.g., Selden & Jeram 1989) which surrounds the food during cheliceral mastication and extraintestinal ingestion.

Anteroventrally directed mouth.—In xiphosurans the mouth is directed posteroventrally, towards the postoral gnathobases from where they receive masticated food (Shultz 1990). Eurypterid mouths have also been re-

constructed with this orientation, and although supportive fossil evidence is weak, the interpretation is probably correct on functional grounds. Mouth orientation of fossil scorpions is unknown. Trilobites were also gnathobasic feeders and had posteroventrally directed mouths. Recent arachnid mouths are all directed anteroventrally, towards the preoral chelicerae. Terrestrialization could have caused a shift from gnathobasic mastication in water to cheliceral mastication on land. Postoral gnathobases along the length of the prosoma are of little use for mastication on land where food would drop from between the coxae. However, a similar function appears to have been retained in the palpal coxae of spiders, adjacent to the mouth, which are used to manipulate food (e.g., Bristowe 1971). Unlike xiphosurans, which trap their food in soft sediments beneath them (Shuster 1950), most arachnids live on an essentially solid substrate and generally catch their food in front of them using anteriorly directed, preoral chelicerae and/or anterior appendages. An anteriorly directed mouth can be interpreted as an adaptation for receiving prey captured preorally by a terrestrial animal.

PARSIMONY AND THE BURDEN OF PROOF

Arachnid monophyly is supported by a number of characters which may represent convergence in response to terrestrialization. These characters can be defended by parsimony and assumed to be homologous and synapomorphic until 'proved' otherwise by a parsimony analysis. Kraus (1998) discussed the limitations of parsimony analysis and argued that characters for phylogeny should be selected and weighted a priori based on structural and functional considerations. We have presented functional arguments to question some of the characters supporting arachnid monophyly. Unfortunately, unequivocal proof for convergent evolution of characters can be difficult to establish, especially when they involve characters in fossil taxa where functional morphology often has to be inferred (e.g., feeding methods in eurypterids) or where empirical data is not available. Our concern is that parsimony is being used to defend weak or inappropriate characters to which considerable objections can be raised. We support Kraus (1998) in questioning whether charac-

ters should be assumed homologous unless detailed arguments in favor of their homology are presented (e.g., our postabdomen character). We worry that in an attempt to compile ever larger databases of characters for parsimony analysis, homologies are being assumed at face value without assessment of character validity. Which is more important, the quantity or the quality of the data used?

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CEPHALOTHORACIC SULCI IN LINYPHIINE SPIDERS (ARANEAE, LINYPHIIDAE, LINYPHIINAE)

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ABSTRACT. Pore-bearing cephalothoracic sulci (pits) are described and illustrated for the first time in several linyphiine spiders (Linyphiidae, Linyphiinae). Sulci are reported in members of the genera *Bathypantes* Menge, *Diplostyla* Emerton, *Kaestneria* Wiehle, *Pacifiphantes* Eskov & Marusik, *Porrhomma* Simon, and *Vesicapalpus* Millidge. The phylogenetic implications of the presence of sulci in linyphiines are discussed.

Members of two lineages of linyphiid spiders (Linyphiidae) typically exhibit cephalothoracic sulci, that is, a pair of grooves or pits of varying shape and depth in the cephalic part of the prosoma (see Hormiga 1994, in press, for references). These two lineages are the Mynogleninae and the Erigoninae.

The mynoglenines are a relatively small clade distributed in Africa (Holm 1968), New Zealand (Blest 1979), and Tasmania and some southern Pacific islands (Hormiga, unpubl. data). Mynoglenine sulci are located on the clypeus (Fig. 1–3), below the anterior lateral eyes and are lined with cuticular openings (pores) that connect to glands with secretory cells that exhibit a unique strategy of membrane amplification (Blest & Taylor 1977; Blest & Pomeroy 1978; Blest 1979). The sulci of mynoglenines are present in adults of both sexes and in juveniles (Blest & Taylor 1977); all known mynoglenines have clypeal sulci. These sulci do not seem to play any active role during the courtship (at least in the species studied by Blest & Pomeroy 1978). It has been suggested that the glands that serve these sulci might elaborate defensive secretions because the unique ultrastructure of the clypeal secretory cells is consistent with the synthesis of a toxic product (Blest & Taylor 1977).

The Erigoninae are the largest clade of linyphiids and are distributed throughout the world except New Zealand (Millidge 1988) and Australia (*contra* Wunderlich 1995; see Platnick 1997:419) which lack native species. One of the most conspicuous characteristics of many (but not all) species of erigonines is the presence in males of a vast morphological di-

versity of cephalic modifications, including lobes, turrets, sulci, pits and modified setae. Erigonine sulci usually have a post-ocular position (Figs. 4, 5) and usually have pores associated with glands that are cytologically different from those of the mynoglenine sulci (Blest & Taylor 1977; Schaible et al. 1986; Schaible & Gack 1987). The sulci and other cephalic modifications of erigonines are found only in adult males and play an active mechanical role during courtship: the sulci are gripped by the female cheliceral fangs, as first noted by Bristowe (1931, 1958).

In this paper I report on the discovery of cephalothoracic sulci in several members of the linyphiid subfamily Linyphiinae, including the well-known Holarctic genus *Bathypantes* Menge. This paper brings to light the presence of these structures in linyphiines but does not attempt to cover exhaustively the distribution and morphological variation of sulci across the Linyphiidae.

METHODS

The morphological observations were carried out using a Leica MZAP0 dissecting microscope and a Leica DMRM compound microscope. All illustrations were done using a camera lucida and inked on drafting film. Specimens examined with the SEM were first transferred to a vial with 75% ethanol and then cleaned ultrasonically for 1–3 minutes. They were then transferred to absolute ethanol and left overnight. Specimens were air dried and then glued to rounded rivets using an acetone solution of polyvinyl resin. Specimens were coated with a carbon base coat followed by a gold-palladium coat for SEM examina-

tion with the AMRAY 1810 of the Smithsonian Institution's SEM Facility. All the specimens studied (see Table 1) are deposited at the National Museum of Natural History (Smithsonian Institution, Washington, D.C.) unless otherwise stated. In addition to those specimens listed in Table 1, I examined *Haplinis diloris* (Urquhart): New Zealand, Fiordland Cascade, in Raoulia, 16 January 1975 (col. & det. A.D. Blest), (Otago Museum, Dunedin) and *Lophomma punctatum* (Blackwall): United Kingdom, Killhope haw., Durham, 2000', 15 June 1966 (J.A.L.C.), (AMNH).

RESULTS

Cephalothoracic sulci were found in all species examined of the linyphiine genera *Bathypantes* (Figs. 6–11), *Diplostyla* Emerton (Figs. 17, 18), *Kaestneria* Wiehle (Figs. 12, 14), *Pacifiphantes* Eskov & Marusik (present only in *P. zakharovi* Eskov & Marusik), *Porrhomma* Simon, and *Vesicapalpus* Millidge (Figs. 15, 16). The sulci were absent in *Linyphantes* Chamberlin & Ivie (five species examined) and in *Pacifiphantes magnificus* (Chamberlin & Ivie) (the males of this latter species remain unknown). The species and specimens studied are given in Table 1. In all these taxa the sulci are located anteriorly in the margin of the carapace, between the chelicerae and the pedipalpal trochanters. The sulcus is a relatively shallow pore-bearing cuticular depression that opens ectoventrally and has an elliptical perimeter (margin). The presence/absence of these pores requires SEM to be discerned. The sulcus is best seen after excision of the pedipalp (e.g., Figs. 6, 9, 15), but in general it can be easily seen without removal of any appendages, particularly from an ectoventral angle. When present, the sulci were found in both males and females of all the 21 species for which both sexes were available for study (see Table 1); no sexual dimorphism in the sulci was discerned with the dissecting microscope.

The morphological details of the sulci of both sexes of *Bathypantes pallidus* (Banks) (Figs. 6–11) and *Kaestneria pullata* (O.P.-C.) (Figs. 12–14) were examined with the SEM. In the female of *Bathypantes pallidus* (Figs. 6–8) the sulci are elliptically shaped (in one specimen the sulcus measured $75 \times 45 \mu\text{m}$). The dorsal and lateral margins of the sulcus

have a slightly sharper edge than the ventral. The sulcus is provided with numerous cuticular pores, particularly in the dorsal half. These pores are not grouped into clusters, as in mynoglennines (Fig. 3), but scattered around, and have a very distinctive wide edge around them (Fig. 8). No cuticular pores can be seen beyond the margin of the sulcus. The sulci of the male of *B. pallidus* (Figs. 9–11) are very similar to those found in females (in one female specimen, Fig. 11, the sulcus measured $78 \times 52 \mu\text{m}$).

The sulci of *Kaestneria pullata* are shallow (Figs. 12–14), particularly in the female, and have a more ventral position under the margin of the carapace. In the females of this species SEM is needed to ascertain the presence of the sulcus which consists of a very shallow depression bearing about 20 cuticular pores (under the dissecting microscope the female sulcus is seen as a slightly darker spot on the cuticle). The male sulcus (Fig. 12) can be seen with the dissecting microscope because the cuticular depression is somewhat deeper than that of the female; in the other aspects these pits are similar to those of the females (Figs. 13–14).

In *Porrhomma convexum* (Westring) the sulci, although shallow, can be clearly seen when viewed under the dissecting microscope. In *Porrhomma borealis* (Banks) (only one female was available for study), *P. montanum* Jackson, *P. microphthalmum* (O.P.-C.) (only males were examined), and *P. pygmaeum* (Blackwall) the sulci are very shallow and oriented ventrally and in both respects are somewhat similar to those of *Kaestneria pullata* (Figs. 12–14).

The sulci of *Pacifiphantes zakharovi* are present in both sexes and are similar, both in position and morphology, to the sulci of *Bathypantes pallidus*.

Males and females of *Lepthyphantes zebra* (Emerton) were examined with the SEM. No cuticular pores were found on the area of the carapace where the sulcus is found in other linyphiines.

DISCUSSION

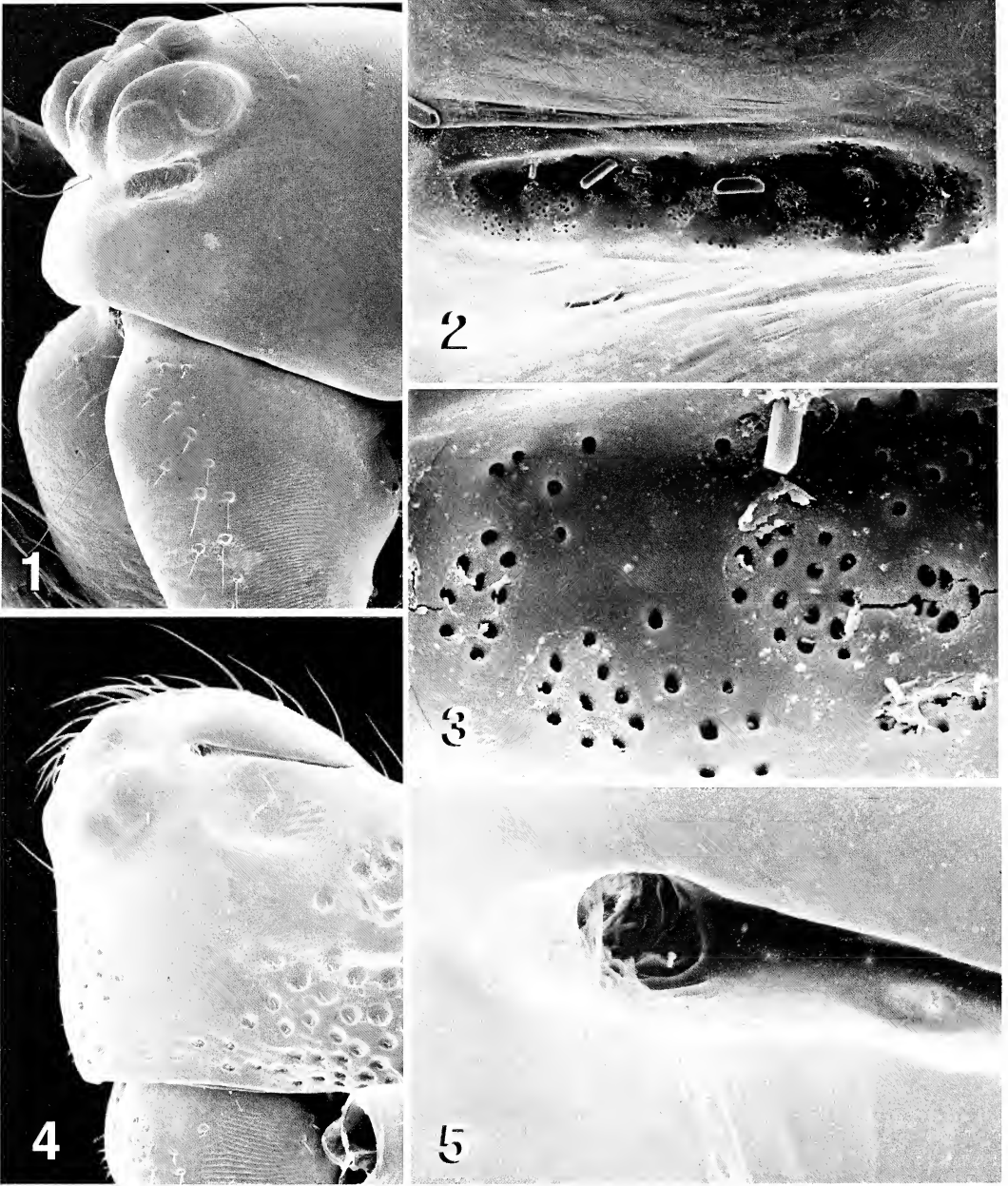
The discovery of cephalothoracic sulci in linyphiines, such as the members of the genus *Bathypantes*, is remarkable because this genus includes some very common spiders (in the Holarctic region) and because these

Table 1.—Taxonomic distribution of cephalothoracic sulci (pits) in the linyphiid taxa studied and specimens examined. “+” indicates sulci present and “-” absent. A “?” indicates that no specimens were available for study; “+?” or “-?” indicates that the observation needs corroboration with scanning electron microscopy (see text for details). Museum abbreviations: AMNH (American Museum of Natural History, New York), CAS (California Academy of Sciences, San Francisco), JZM (J. Zujko-Miller private collection), USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C.), ZMUK (Zoological Museum, University of Copenhagen, Copenhagen).

Species	Male sulcus	Female sulcus	Country, State or Province	Locality	Collection Date(s)	Museum
<i>Bathyphanter alascensis</i> Banks	+	+	USA, Oregon	Siuslaw Natl. Forest	14 July 1990	USNM
<i>Bathyphanter approximatus</i> (O. P.-C.)	+	+	Washington	Butler Hill	10 December 1988	USNM
			Denmark	Brenerholmsaret	13 July 1920	ZMUC
<i>Bathyphanter alboventris</i> (Banks)	?	+	USA, Tennessee	Rainbow Cave	8 August 1981	USNM
<i>Bathyphanter bishopi</i> (Ivie)	+	+	USA, North Carolina	Great Smoky Mts. N.P.	7 August 1961	USNM
<i>Bathyphanter brevipes</i> (Emerton)	+	+	USA, Washington	Thurston Co., Evergreen State College	16 December 1993	JZM
<i>Bathyphanter eumenis</i> (L. Koch)	+	+	Russia, NE Siberia	Kamchatka	17 September 1996	USNM
<i>Bathyphanter gracilis</i> (Menge)	+	+	Russia, NE Siberia	Kamchatka	18 September 1996	USNM
<i>Bathyphanter keeni</i> (Emerton)	+	+	USA, California	Mendocino woodlands	20 August 1990	USNM
			Canada, Brit. Col.	Vancouver	4-9 July 1988	USNM
<i>Bathyphanter nigrinus</i> (Westring)	+	+	Denmark	Copenhagen	September 1989	ZMUC
<i>Bathyphanter orica</i> Ivie	?	+	USA, Washington	Thurston Co., Evergreen State College	25 October 1992	JZM
<i>Bathyphanter pallidus</i> (Banks)	+	+	USA, Maryland	Patuxent Wildlife Refuge Center	2 June 1994	USNM
<i>Bathyphanter pogonias</i> Kulczynski	+	+	Russia, Kurile Isles	Bering Isld	July-August 1987	USNM
<i>Bathyphanter reprobis</i> (Kulczynski)	?	+	Russia, NE Siberia	Lankovaya River	12-19 August 1992	USNM
<i>Bathyphanter setiger</i> (F. O. P.-C.)	+	?	Denmark	Losø, Blødens vestide	20 July 1946	ZMUC
<i>Bathyphanter similinus</i> (L. Koch)	?	+	Denmark	Greenland, Disko	9 July 1962	ZMUC
<i>Bathyphanter waneta</i> Ivie	+	+	USA, Washington	Brooks Mem. State Pk.	1 March 1980	USNM
<i>Bathyphanter weyeri</i> (Emerton)	+	+	USA, West Virginia	W. Va. Univ. Forest	26 June-9 July 1989	USNM
<i>Bathyphanter</i> sp. Oregon	?	+	USA, Oregon	Shore Acres State Pk.	16 August 1990	USNM
<i>Diplostyla concolor</i> (Wider)	+	+	USA, Massachusetts	Quisset	10 June 1988	USNM
<i>Kaestneria dorsalis</i> (Wider)	-?	-?	Sweden	Sjögarn, Gotland	14 July 1936	ZMUC
<i>Kaestneria pullata</i> (O.P.-C.)	+	+	Russia, NE Siberia	Lankovaya River	12-19 August 1992	USNM
<i>Pacificphantes magnificus</i> (Ch. & Ivie)	?	-	USA, Washington	5 mi. E of McCleary	26 August 1952	AMNH

Table 1.—Continued

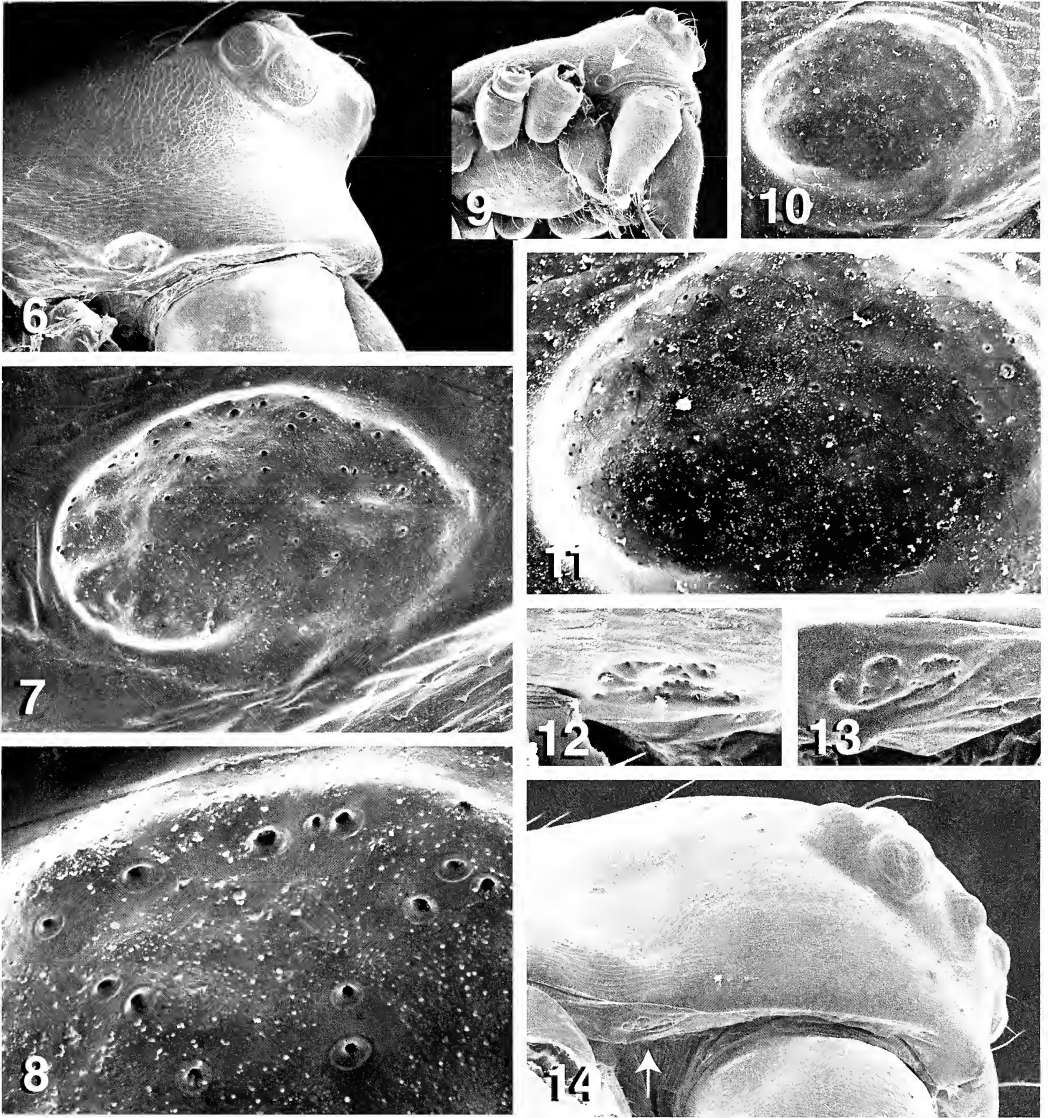
Species	Male sulcus	Female sulcus	Country, State or Province	Locality	Collection Date(s)	Museum
<i>Pacipiphantes zakharovi</i> Eskov & Marusik	+	+	Russia	Vladivostok	30 September 1997	USNM
<i>Porrhonma borealis</i> (Banks)	?	+	Russia, NE Siberia	Magadan Area, Ola Riv. Upper flow	15–18 September 1992	USNM
<i>Porrhonma convexus</i> (Westring)	+	+	Iceland	Molifellsa, Skagafj	13 July 1933	ZMUC
<i>Porrhonma montanum</i> Jackson	+	+	Denmark	Hestheaven, Rønde	July–September 1994	ZMUC
<i>Porrhonma microptalmum</i> (O.P.-C.)	+	?	Denmark	Hestheaven, Rønde	July–September 1994	ZMUC
<i>Porrhonma pygmaeum</i> (Blackwall)	+	+	Denmark	Zealand, Tisvildeleje	19–20 May 1991	ZMUC
<i>Vesicapalpus simplex</i> Millidge	+	+	Brazil	Parque Nacional da Serra dos Orgãos	11 November 1959	AMNH
<i>Vesicapalpus</i> sp. Colombia	+	+	Colombia, Huila	P.N.N. Puracé, Laguna de San Rafael	15 February 1998	USNM
<i>Lepthyphantes zebra</i> (Emerton)	–	–	USA, Georgia	Ellicott Rock Wilderness Area	24 May 1993	USNM
<i>Linyphantes aeronauticus</i> (Petrunkevitch)	–	–	USA, Washington	Douglas Co., Hw2, mi. 135 rest stop at Lake Entiat	20 March 1980	USNM
<i>Linyphantes anacortes</i> Chamberlin & Ivie	–	–	USA, Oregon	Curry Co., Brookings	19 June 1952	USNM
<i>Linyphantes orcinus</i> (Emerton)	–	–	USA, Washington	Clallam Co., Salt Creek mouth	23 May 1987	USNM
<i>Linyphantes pualla</i> Chamberlin & Ivie	–	–	USA, Washington	Mason Co., Brown Creek	15 October 1993	JZM
<i>Linyphantes victoria</i> Chamberlin & Ivie	–	–	USA, Washington	Horse Camp Thurston Co., Evergreen State College	25–27 October 1992	JZM



Figures 1-5.—Cephalothoracic sulci in Linyphiidae. 1. *Haplinis diloris* (Urquhart) (Mynogleninae), female, lateral; 2, 3. Detail of *Haplinis diloris* male lateral subocular sulcus (right); 4. *Lophomma punctatum* (Blackwall) (Erigoninae), male, lateral; 5. Detail of *Lophomma punctatum* male postocular sulcus (left).

pits are easily observable with the dissecting microscope. Consequently I was very reluctant to believe that these distinct structures remained undescribed. The only taxonomic revision of *Bathypantes* is that of Ivie (1969) for Nearctic species. In his monograph Ivie described and illustrated 27 spe-

cies of *Bathypantes* (some of them are currently classified in other genera), but he made no reference to the sulci. None of the many isolated taxonomic descriptions of *Bathypantes*, *Diplostyla*, *Porrhomma*, and *Vesicapalpus* species I have checked mention these pits. It is difficult to explain how such



Figures 6–14.—Cephalothoracic sulci in Linyphiidae. 6. *Bathyphantes pallidus* (Banks), female, lateral; 7. *Bathyphantes pallidus*, female sulcus (right); 8. Detail of *Bathyphantes pallidus* female sulcus (right); 9. *Bathyphantes pallidus*, male, ventrolateral (arrow points to sulcus); 10. *Bathyphantes pallidus*, male sulcus (right); 11. Detail of *Bathyphantes pallidus* male sulcus (right); 12. *Kaestneria pullata* (O.P.-C.), male cuticular pores (right); 13. *Kaestneria pullata*, female cuticular pores (right); 14. *Kaestneria pullata*, female, ventrolateral (arrow points to location of cuticular pores).

a conspicuous structure has remained undocumented for so long.

The presence of cephalothoracic pore-bearing cuticular depressions in linyphiines is of relevance for the study of the evolution of cephalic specializations. Unfortunately, detailed understanding of the evolutionary history of these structures is severely hindered by the lack of explicit hypotheses on the phyloge-

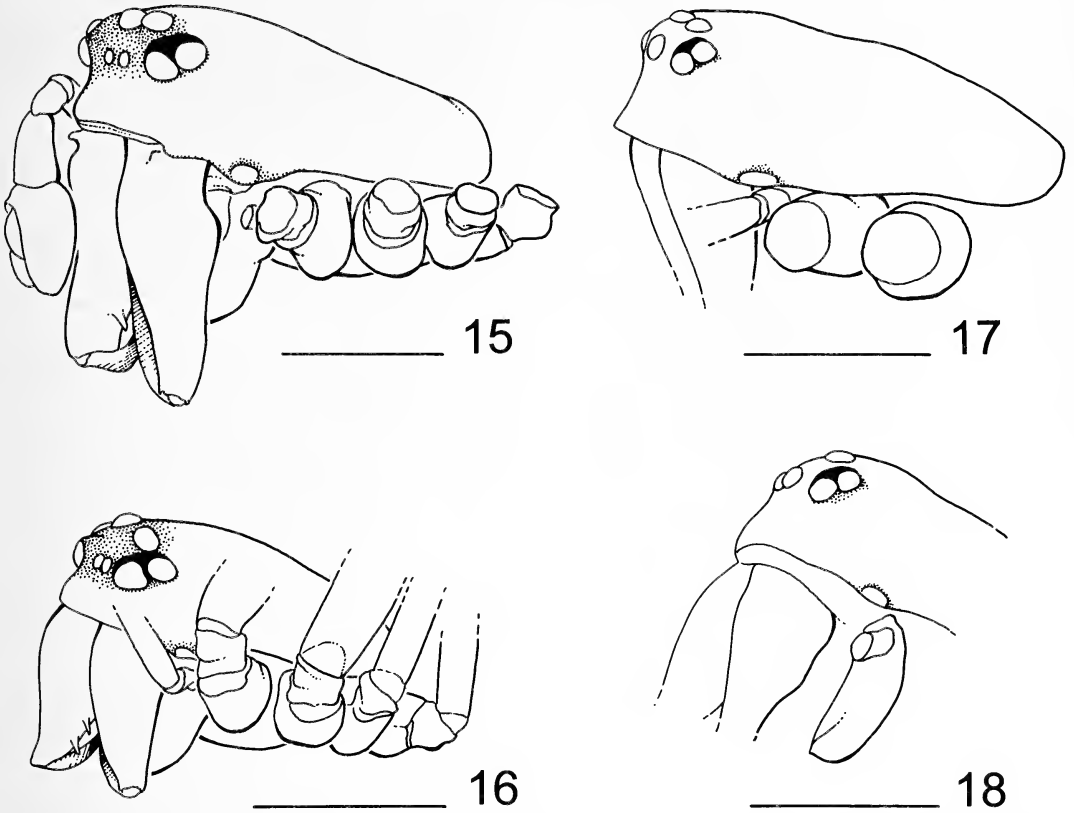
netic structure of the Linyphiidae. In my opinion, one of the main questions concerning the evolution of linyphiid sulci is whether mynogenine and erigonine sulci are homologous structures, as argued by Blest (1979), Blest & Taylor (1977), Blest & Pomeroy (1978) and Millidge (1993). In an initial assessment of this problem (Hormiga 1994) I concluded that although the non-homology hypothesis was

more parsimonious, the question could not be rigorously tested "until more data (taxa, particularly those with any type of sulci and/or glands, and information on the glands)" were studied. Recent progress in the phylogenetics of erigonines (Hormiga in press) supports the non-homology hypothesis of the erigonine and mynoglennine sulci. This is a result of the basal cladistic placement (within the Erigoninae) of a number of lineages in which neither the cuticular pores nor the sulci are present. Given such a cladogram topology parsimony requires independent origins (i.e., non-homology) of the sulci in erigonines and mynoglennines; this occurs even when the cuticular pores of erigonines and mynoglennines are coded as homologous in the cladistic analysis. The discovery of sulci in linyphiines suggests that this "character" is even more homoplasious than initially argued because several independent origins of sulci in the Linyphiidae are required: one in mynoglennines, at least two in erigonines, and one or more instances in linyphiines (unless mynoglennine and linyphiine sulci are homologous). All described mynoglennines have subocular sulci (Blest 1979), and the presence of such sulci (and their associated glands) is synapomorphic for this subfamily (Hormiga 1994, in press). The phylogenetic patterns of sulci and cuticular pores in erigonines are much more complex (Hormiga in press) and our knowledge is still very preliminary. Despite this, it seems that based on the taxonomic distribution of these characters and on my cladistic reconstructions, there are multiple origins of the prosomic cuticular pores and at least two independent origins for sulci in erigonines (pores are more widely distributed across taxa than sulci).

In linyphiines prosomic cuticular pores had been described in *Bolyphantes* (Blest & Taylor 1977). In *B. luteolus* (Blackwall) pores are found both in the male and the female (*contra* Blest & Taylor 1977: 91) (Hormiga in press). So far no cephalothoracic sulci have been documented in linyphiines (other than those described in this paper). Because there is no explicit cladistic hypothesis for the genera (or an adequate subset of genera) of Linyphiinae, at the present time it is not possible to provide a robust hypothesis about the origin of the sulci within this subfamily. Nevertheless the genera *Bathyphantes*, *Diplostyla* and *Kaestneria* have been traditionally considered close rela-

tives (this has been largely based on overall similarity; e.g., Wiehle (1956) or Millidge (1984)), and several species of these genera have changed generic placement within this cluster of genera. The presence of cephalothoracic sulci in *Bathyphantes*, *Diplostyla*, *Kaestneria*, and *Porrhomma* is a derived trait and thus a potential putative synapomorphy supporting the monophyly of these genera. The genitalic morphology of these four genera seems to be consistent with this hypothesis (e.g., Millidge 1977), but this requires further study and testing. Chamberlin & Ivie (1942: 45) and Ivie (1969: 2) suggested that *Bathyphantes* and *Linyphantes* were closely related because they agree in "in most general characters." The five species of *Linyphantes* that I have examined, including the type species *L. aeronauticus* (Petrunkévitch), lack sulci and their palp morphology shares little in common with the palp morphology of *Bathyphantes*. To this date no synapomorphies have yet been proposed that could potentially support the monophyly of *Linyphantes* plus *Bathyphantes*. *Pacifiphantes magnificus*, recently transferred from *Bathyphantes* by Eskov & Marusik (1994) using phenetic criteria, also lacks sulci (although males remain unknown) although the pits are present in the both sexes of the type species, *Pacifiphantes zakharovi*. The phylogenetic placement of *Vesicapalpus* remains even more obscure. This monotypic Neotropical genus is known in the literature after a single male specimen (the holotype of *Vesicapalpus simplex* Millidge). Millidge (1991) did not document the presence of sulci in his sparse description of *V. simplex*. Sulci are present in both sexes of *Vesicapalpus simplex* (Figs. 15, 16) and in an undescribed species from Colombia (Hormiga unpubl. data). Whether the sulci of *Vesicapalpus* are or not homologous to the sulci of other linyphiines cannot be answered in absence of a phylogenetic hypothesis for the relationships of these taxa.

Outside Linyphiidae, but within Araneidea, similar pore-bearing sulci are found in most members of the family Anapidae (Platnick & Forster 1986, 1989, 1990). Platnick & Forster (1989: 135) suggest that the presence in both sexes of glandular openings at the anterolateral corners of the carapace may be a synapomorphy of Anapidae. The cuticular openings of anapids are located in a pit on the



Figures 15–18.—Cephalothoracic sulci in Linyphiidae. 15. *Vesicapalpus simplex* (Millidge), male (holotype) from Argentina (right side reversed); 16. *Vesicapalpus simplex* female from Brazil; 17. *Diplostyla concolor* (Wider), male from Massachusetts; 18. *Diplostyla concolor*, female from Massachusetts. (Scale bars = 0.5 mm)

edge of the carapace, just above the endites (see figs. 1–4 in Platnick & Forster 1986). In *Minanapis* Platnick & Forster there is no pit and the pores open directly on the surface of the carapace. In other anapids, such as *Gertschanapis* Platnick & Forster and *Maxanapis* Platnick & Forster, the cephalic pit has shifted onto a separate sclerite that is reflexed under the lateral margin of the carapace (Platnick & Forster 1989, 1990) in an analogous situation to the condition found in *Kaestneria pullata* (cf. figs. 271 and 272 in Platnick & Forster 1989).

In sum, the pore-bearing sulci of linyphines provide another instance of homoplasy in the evolution of cephalic specializations in linyphiids. Preliminary data presented here suggests that the study of this character will be important for phylogenetic reconstruction. Progress in understanding the evolutionary chronicle of these complex character systems

will have to wait for more data on their biological role and function (at present, the function of the sulci in mynoglennines and linyphines remains unknown), for more information on its taxonomic distribution, and for a more detailed understanding of the higher level phylogenetics of this large group of araneoid spiders.

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SPERMATOPHORES AND THE EVOLUTION OF FEMALE GENITALIA IN WHIP SPIDERS (CHELICERATA, AMBLYPYGI)

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ABSTRACT. Whip spiders use stalked spermatophores for sperm transfer. These are complex structures, and their morphology varies among genera and families. Usually, the paired sperm masses hidden within the spermatophores are small, and there has been a co-evolution of spermatophores and those parts of the female genitalia which are used to pick up the spermatozoa and to store spermatozoa. These are structures like specialized sclerotizations, glands or, in a few species, seminal receptacles which are hidden inside the genital atrium (or uterus externus). In most species there are paired erectile bodies, homologous to genital appendages, which are attached to the dorsal side of the genital operculum which also is part of an appendage homologon. All these structures vary among genera and families. The comparison of spermatophores and genitalia of different species belonging to most genera and families suggest that the female gonopods consist primarily of paired cushion-like structures, each equipped with a small finger-like appendage vestige. These appendage vestiges are retained in many species, particular in the Charinidae and Charontidae. They are erectile by increase in blood pressure, and they are thereby probably bent in characteristic ways and thus can pull off the sperm masses from the spermatophore. In some Charinidae, and in some species of *Damon* and *Phrynichus* (Phrynida, Phrynichidae) these appendage vestiges are totally lost. In the Phrynidae, on the other hand, they have become sclerotized and hard. They form the well-known claw-like sclerites, and an invagination at the base of each sclerite has been shaped to form a true seminal receptacle. Similar genitalia have evolved convergently in the genus *Trichodamon* (Phrynida, Phrynichidae). Spermatophores and the corresponding female genitalia and their mechanisms of a number of genera from most families are described and illustrated.

Whip spiders transfer spermatozoa by means of stalked spermatophores (Alexander 1962a, b; Klingel 1963; Weygoldt 1969). After a prolonged courtship dance which the male performs in front of the female, he turns around until facing the same direction as the female and standing in front of her. In this position he deposits a spermatophore and attaches its stalk to the substratum. Thereafter he turns around to face the female and lures her toward the spermatophore. The female then steps over the spermatophore and picks up the sperm.

The spermatophores are large and complex structures. They consist of a stalk, a spermatophore head and paired sperm masses or, in other species, sperm packages. Each individual spermatozoon is rolled up and encapsulated, and the globular cells are either glued together or surrounded by secretion. The sperm masses are small when compared to the size of the total spermatophore. Spermatophore morphology varies between species,

genera and families, and the same is true for the female genitalia, in particular for those structures which are used to pick up the spermatozoa. After sperm transfer, an empty spermatophore is left behind or, in a few species, is eaten either by the male or the female.

The distal genitalia of a whip spider of either sex are composed of a large genital atrium, homologous to the uterus externus of spiders, a large genital operculum, and paired erectile bodies attached to the dorsal or inner side of the genital operculum (Weygoldt et al. 1972). These erectile bodies are considered to be homologous to genital appendages, to the endopods of the opisthosomal appendages of eurypterids or xiphosurids (Pocock 1894; Werner 1935; Weygoldt 1970); they are therefore termed gonopods here. The genital operculum with its lateral book lungs is homologous to the genital operculum of xiphosurids and eurypterids which is part of the same pair of appendages, the book lungs or, in xiphosurids the book gills, representing the exopods.

In the male, the gonopods are two-segmented. They form an unpaired complex structure provided with muscles and haemolymph spaces and a complex central cavity which acts as a mold for the formation of the spermatophore head. It also contains grooves through which the secretions from several large glands can be lead to the exterior in order to attach the spermatophore stalk to the ground. Kraus (1970) suggested that the shape of the male genitalia could provide useful characters for taxonomy. The problem is that the shape of these organs depend heavily on the state of preservation. Genitalia of two males of the same species sometimes appear much more different from each other than those from two males of two different species. The spermatophores formed in these male genitalia are complex and diverse. Their sperm masses are located at various positions within the spermatophore head. Unfortunately the spermatophores of only a limited number of species are known. They will be described subsequently.

The female genitalia are much simpler. The genital atrium contains specialized sclerotizations which vary among species, glandular structures and various structures used for sperm storage. Even true seminal receptacles have evolved convergently in some groups. The gonopods are cushion-like structures with or without vestiges of the appendage telopodids. These telopodids, here termed appendage vestiges, are used to pick up the sperm mass from the spermatophores. Their morphology varies considerably between species, genera and families. Just as with male copulatory organs, there has been a co-evolution of spermatophores and female genitalia.

All whip spiders will mate several times if they have the chance. The females become unreceptive once oogenesis has reached a certain stage. All whip spiders are long-lived and continue to molt and to grow after having reached sexual maturity. During molting, the females loose all stored spermatozoa—which remain in the shed storage organs. The females become receptive again soon after molting.

In the following discussion I will demonstrate different types of spermatophores and the corresponding female genitalia and describe how these are used to pick up the sperm masses and how they have evolved within the

taxon Amblypygi. As to the function, most of my description is inferred from the morphology of the structures. Many whip spiders are unable to walk and to mate on glass; therefore, direct observation is impossible.

As a base for the discussion of the evolution of genitalia I use the cladogram and system of Weygoldt (1996a, b) (Table 1). In this system, the African genus *Paracharon* is considered the sister group of the remaining amblypygids, the Euamblypygi. This group is divided into two taxa, the Charinidae and the Neoamblypygi. The Charinidae is mainly characterized by plesiomorphies; I have not found convincing synapomorphies. All charinid genera are in urgent need of revision. In particular, it is not clear whether *Charinus* Simon 1892 is a monophyletic group and whether *Charinides* Gravely 1911 should be considered a junior synonym of *Charinus* as Delle Cave (1986) assumes. The Neoamblypygi, however, is united by several synapomorphies. It contains the taxa Charontidae as restricted by Quintero (1986) and the Phrynida or Apulvillata, and these are divided into the Phrynidae and Phrynichidae, both characterized and united by convincing synapomorphies.

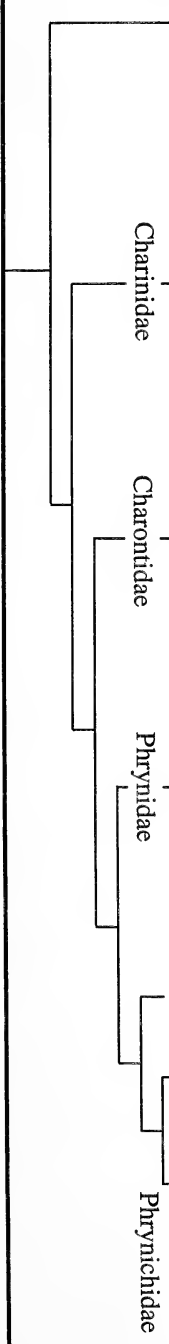
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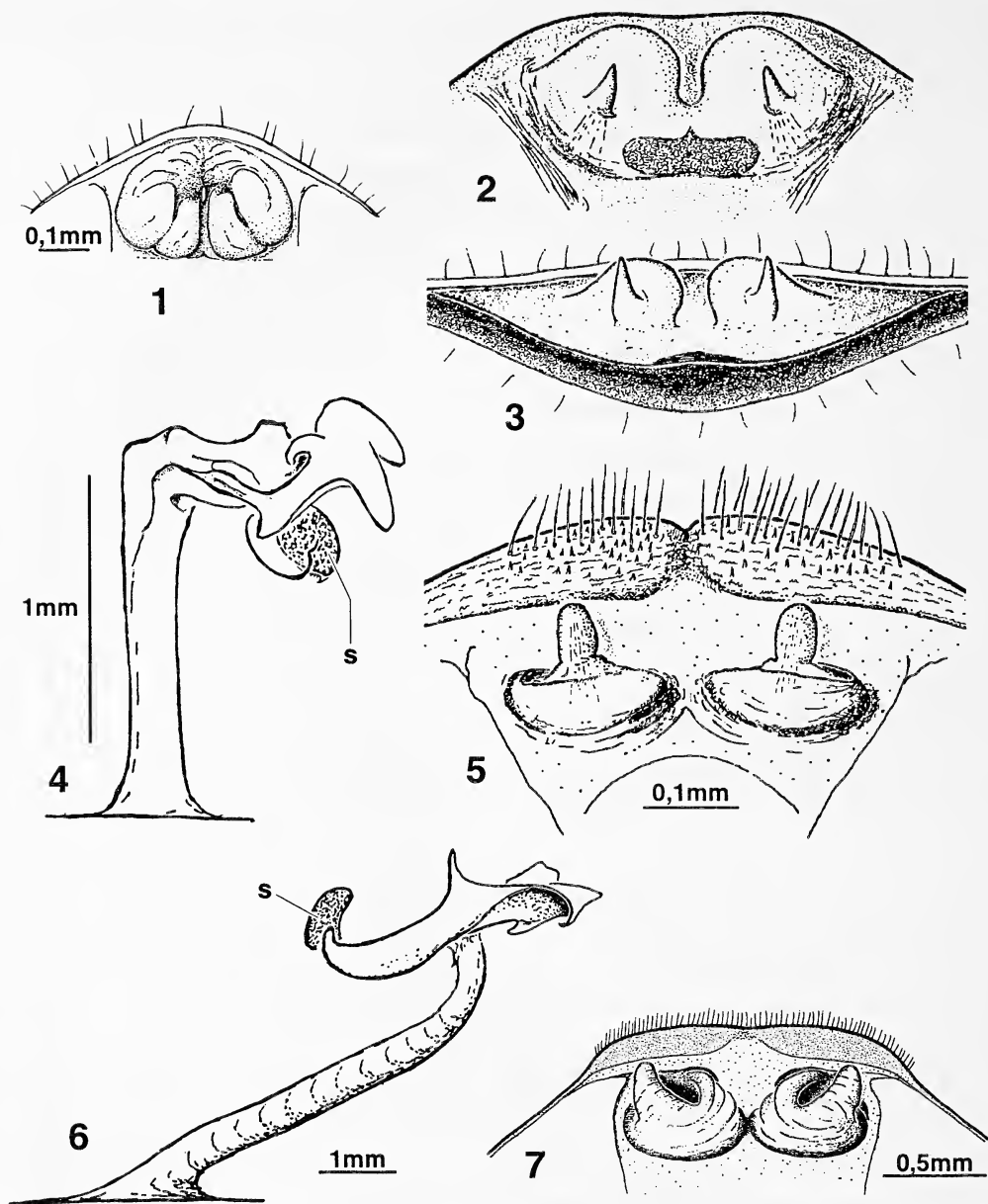
***Paracharon*.**—According to the taxonomic analysis, *Paracharon caecus* Hansen 1921 is the most plesiomorphic species and the adelphotaxon of all remaining Amblypygi, the Euamblypygi. Its female gonopods are simple soft cushions (Fig. 1). Spermatophores are not known, therefore the function of the gonopods are unclear; and it is also unclear whether the simple gonopods are plesiomorphic or the result of simplification.

Charinidae and Charontidae.—Gonopods with a soft, finger-like appendage vestige (Fig. 2, 3) are found in many charinid and charontid whip spiders. They are probably synapomorphic for the Euamblypygi or, if the genitalia of *Paracharon* are secondarily simplified, for all Amblypygi.

Such finger-like appendage vestiges as shown in Fig. 2, 3 for *Charinus koepkei* Weygoldt 1972c may be short and pointed as in this case and in *Charinides bengalensis* Gravely 1911 or much longer as in several other *Charinus* species, e.g., *Charinus africanus* Hansen 1921 (Weygoldt 1972a). The

Table 1.—The amblypygid genera, their relationships according to Weygoldt (1996a and 1996b), their distribution, and species numbers. The species numbers for many genera are guesses based on descriptions from the last century. Only for the Phrynidae and Phrynichidae can reliable data be given; they are based on the revisions of Mullinex (1975), Quintero (1981, 1983, a few more species have been described since then), Weygoldt (1998) and the author's unpublished data on *Damon*.

Genera		Distribution	No. of species	
	Paracharon	W. Africa	1	
	Charinidae	Sarax	S.-E. Asia	4(?)
		Phrynichosarax	S.-E. Asia	5(?)
		Charinus	world wide	>20
		Charinides	circumtropic	5(?)
		Tricharinus	neotropic	3
		Catageus	S.-E. Asia	1
	Charontidae	Charon	S.-E. Asia	>4
		Stygophrynus	S.-E. Asia	6(?)
	Phrynidae	Acanthophrynus	Mesoamerica	1
		Phrynus	Mesoamerica	>16
		Paraphrynus	Mesoamerica	>12
		Heterophrynus	S. America	10(?)
Phrynichidae	? — Xerophrynus	S.-E. Africa	1	
	Phrynichodamon	S.-E. Africa	1	
	Damon	Africa	10	
	? — Musicodamon	N. Africa	1	
	Trichodamon	S. America	2	
	Phrynichus	Africa, Asia	14	
Euphrynichus	Africa	2		



Figures 1-7.—Female genitalia and spermatophores of some charinid and charontid Amblypygi. 1. Female genitalia of *Pracharon caecus*; dorsal aspect; 2. Female genitalia of *Charinus koepkei*, dorsal aspect; 3. Same, posterior aspect (from Weygoldt 1972c); 4. Spermatophore of *Sarax sarawakensis* in lateral view; 5. Female genitalia of *Sarax sarawakensis*, dorsal aspect; 6. Spermatophore of *Stygophrynus longispina*; 7. Female genitalia of *Stygophrynus longispina*, dorsal aspect. (s = sperm mass).

actual appearance may vary between specimens, depending on the state of preservation or on haemolymph pressure during preservation. For most species, spermatophores are not known. It is most likely that the finger-like appendage vestiges of the gonopods can be elongated or erected by an increase in hae-

molymph pressure and withdrawn by muscles, and that they are bent and strengthened in a species specific way and thus can pull off the protruding sperm masses during sperm transfer.

However, a few examples have been studied. In *Sarax sarawakensis* (Thorell 1888)

(Charinidae), the spermatophore head is complex, with paired wing-like appendages of which the functional significance is obscure. They probably provide the necessary stimuli for the gonopods to find the two protruding sperm masses (Fig. 4) (Weygoldt 1990). The inactive gonopods are rounded in this species (Fig. 5), but it is likely that they can also be elongated and pull off the sperm masses during sperm transfer. The situation is similar in *Stygophrynus longispina* Gravely 1915 (Neoamblypygi, Charontidae). Its spermatophore (Fig. 6) (Weygoldt 1990) also carries two protruding sperm masses. They are mounted on the distal ends (viewed from the male) of the spermatophore head. The spermatophore stalk is inserted at about the center of the spermatophore head. Thus, when the female presses down the proximal end of the spermatophore head with her genital operculum, the distal end will raise and move the sperm masses into the female gonopore. The folded appearance of the female genitalia and its appendage vestiges (Fig. 7) suggest that these can be inflated considerably and can tear off the sperm packages during sperm transfer.

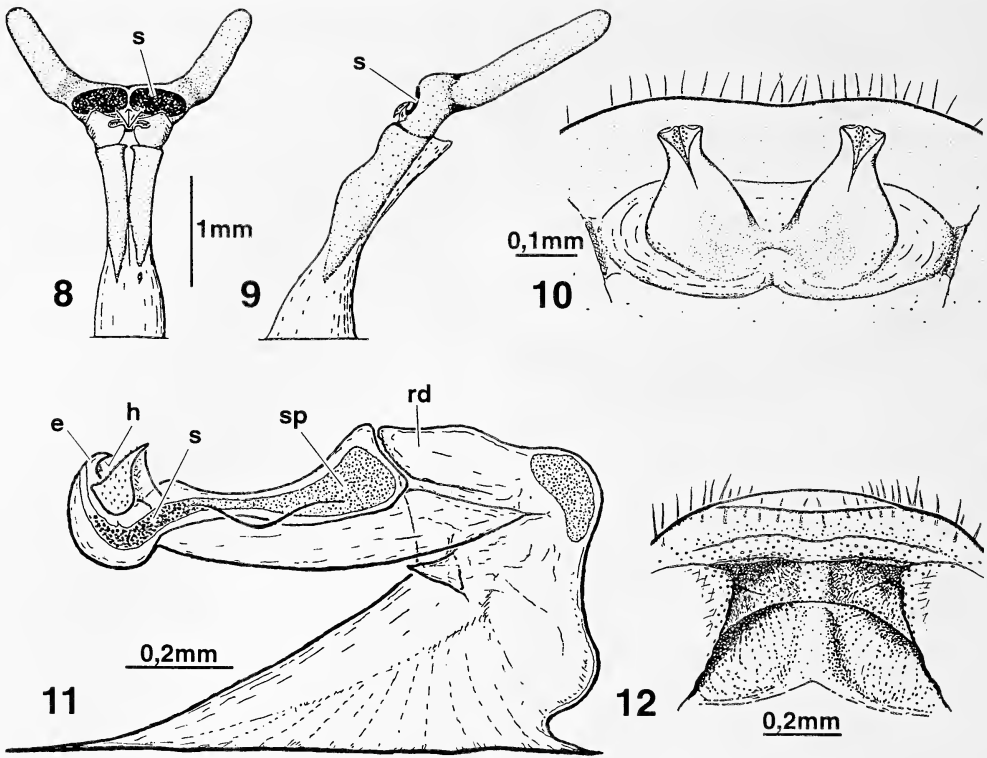
Charinus is a large genus distributed circumtropically over all continents and also occurring on islands, even volcanic ones like Galapagos. Some species have evolved different spermatophores, different genitalia and different means of sperm transfer. In the Brazilian species *C. brasiliensis* Weygoldt 1972 and *C. montanus* Weygoldt 1972, the appendage vestiges of the genitalia are enlarged and thickened and have the appearance of sucker-like or prehensile structures (Weygoldt 1972a, b) (Fig. 10). They can be extended by increase in haemolymph pressure and retracted by strong muscles. The spermatophores are also different. They are quite simple (Figs. 8, 9), and the spermatozoa do not form compact, protruding sperm masses but flat layers at the base of the spermatophore head (Weygoldt 1972b, 1974a). The female picks up the spermatozoa by means of her sucker-like genitalia. They are then stored in two distal cavities of the genital atrium directly behind the ends of the genitalia.

The situation is even more different in *Charinus seychellarum* Kraepelin 1898. The genitalia are reduced to flat cushions in front of which the floor of the genital atrium and its roof are strongly sclerotized. There is no

erectile appendage vestige. Further, the posterior margin of the genital operculum is transparent and forms a hard and sharp edge (Fig. 12). The spermatophore is unique among amblypygids (Fig. 11). There is a strong, triangular stalk which firmly attaches the structure to the ground, even to sand. The spermatophore head consists of a flat plate carrying two strong sperm packages, each with a spacious sperm reservoir and an opening at its tip. This tip is bent upwards and forms an embolus armed with two small hooks. The reservoirs of both sperm packages join proximally; here they contain no spermatozoa but a swelling substance which, on contact with aqueous solutions, presses out the spermatozoa stored distally. This is one mechanism. There is another, more important mechanism: The flat plate carrying the sperm packages acts as a spring. If the whole structure is bent upwards distally, it arrests at about 45°, and two rod-like structures at the upper part of the spermatophore stalk act as pistons pressing out the sperm masses. During sperm transfer, the female attaches the sharp edge of the margin of her genital operculum under the hooks of the emboli and then bends the sperm package upwards. The spermatozoa are thereby emptied into the genital atrium and stored between the roof of the atrium and a dorsal fold.

Phrynida.—The situation in the Phrynida or Apulvillata is much clearer. This taxon contains two families, the Phrynidae and the Phrynichidae.

Phrynidae.—In the Neotropical Phrynidae, the female gonopods are equipped each with a claw-like, hard and dark sclerite (Fig. 13). These sclerites have long been known and termed cocoon-holders by Börner (Werner 1935). They have, however, nothing to do with the transportation of the egg sac. The sclerites can be elevated by increase in haemolymph pressure. They are further equipped with a strong adductor muscle which, by superficial view, seems to be attached to a deep apodeme. However, at the base of each sclerite there is an invagination leading into a spacious seminal receptacle (Fig. 14). The apertures of these receptacles are covered by the sclerite bases, and the adductor muscles are attached to the walls of the receptacles (Fig. 15). Contraction of these muscles, thus, leads to the adduction of the sclerites and at the



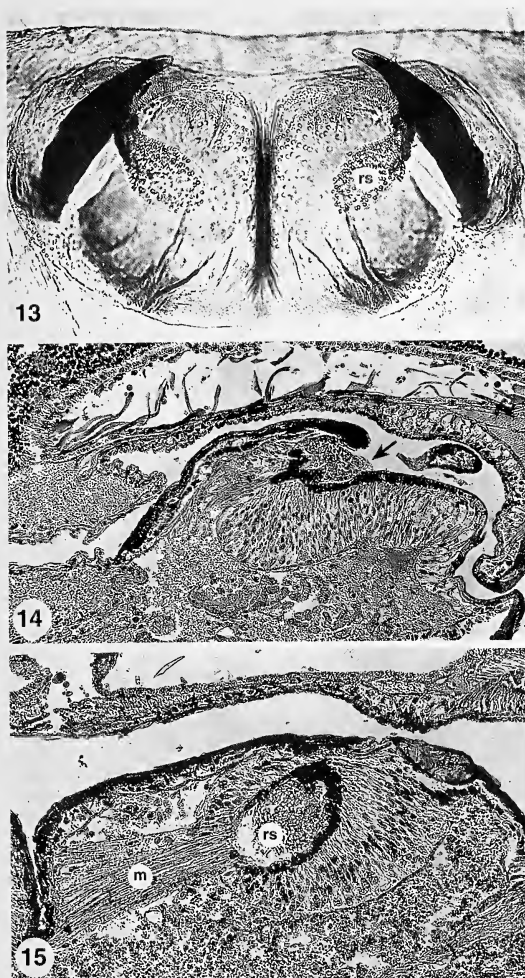
Figures 8–12.—Spermatophores and female genitalia of two species of *Charinus*. 8. Spermatophore of *C. brasilianus*, anterior view; 9. Same, lateral aspect; 10. Female genitalia of *C. brasilianus*, dorsal aspect (from Weygoldt 1972b); 11. Spermatophore of *C. seychellaraum*, lateral view; 12. Female genitalia of *C. seychellaraum*, dorsal aspect. Abbreviations: e = embolus, h = hooks, rd = rod-like structure which compresses the sperm package when the tip is lifted upwards. Abbreviations: s = sperm mass, sp = sperm package).

same time widens the seminal receptacles. The walls of the receptacles are punctured by many glandular pores. Nutrients or other substances are probably released through these pores and nourish or otherwise maintain the spermatozoa (Weygoldt et al. 1972).

The males of the Phrynidae produce large spermatophores with triangular, heavily sculptured spermatophore heads (Weygoldt 1969, 1972b, 1974b, 1977) (Figs. 16, 17, 19, 20). The formation of these complex spermatophores takes quite long, 10–20 minutes. After spermatophore formation, the male turns toward the female again and touches for another 10 minutes the spermatophore with his pedipalps and chelicerae. The meaning of this behavior is still obscure. The attachments of a pheromone may be one possibility, the deposition of an enzyme to soften the sperm packages another. The spermatophore contains two comparatively small sperm-packages hidden

deeply among the sculpturing (Figs. 17, 18, 19, 21), and two arm-like distal extensions act as conductors leading towards the sperm-packages. The female pulls out these sperm-packages by means of her claw-like sclerites, and the sperm is thereby sucked into the seminal receptacles. In *Phrynus marginemaculatus* C.L. Koch 1841, the sperm packages are attached to small plates, and these plates are visible pressed underneath the claw-like sclerites after sperm transfer.

The sculpturing varies among species and also the shapes of the arm-like appendages; and they may even be forked or T-shaped. The functional significance of these differences is obscure, in particular since the female genitalia are quite uniform. We may assume that the different sculpturings aid the female in recognizing the spermatophore and finding the sperm packages. Another point may be that the sculpturing creates a large, hard, elastic



Figures 13–15.—Female genitalia of *Phrynus marginemaculatus*; 13. Dorsal aspect of genitalia of an exuvia with the claw-like sclerites; 14. Longitudinal section through one of the gonopods with the entrance to the seminal receptacle (arrow); 15. Cross section through one of the gonopods with the seminal receptacle containing spermatozoa. Abbreviations: m = muscle, rs = seminal receptacle (from Weygoldt et al. 1972).

spermatophore head with a minimum of material. Even the stalk is created with a minimum of material; it is not solid as may seem from Figs. 16 and 20 but its cross section is V-shaped instead.

This unique system featuring spermatophores with complexly sculptured spermatophore heads and female gonopods equipped with claw-like sclerites and seminal receptacles is one of the autapomorphies of the Phrynidae. The features are found with little

variation in all four genera and in all species (Mullinex 1975; Quintero 1981; Weygoldt 1972b, 1974b, 1977).

Phrynichidae.—The Phrynichidae are much more variable as far as their spermatophores and genitalia are concerned.

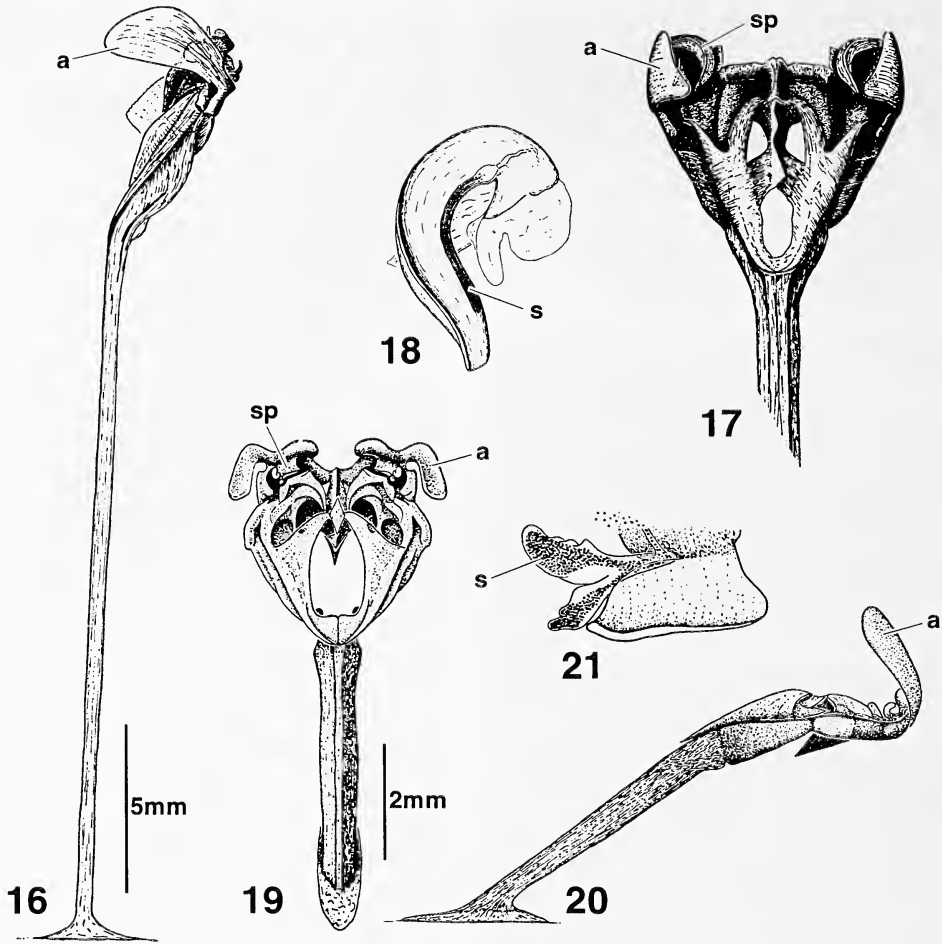
Phrynichodamon scullyi (Purcell 1911) is a primitive species and the sister taxon of all other Phrynichidae (Weygoldt 1996a) (with the exception of *Xerophrynus* Weygoldt 1996, which is tentatively considered a basal offshot of the Phrynichidae, Table 1). Spermatophores and genitalia of this species resemble the situation found in charinid and charontid whip spiders. In the small and simple spermatophores, the spermatozoa form large, protruding sperm masses (Weygoldt 1998a). The female gonopods are equipped with soft, finger-like appendage vestiges which can probably be extended by haemolymph pressure and tear off the sperm masses. These are then stored underneath the appendage vestiges (Weygoldt 1996a) (Fig. 23).

It is easy to conceive that a remote ancestor of the Phrynidae had a similar system and that the appendage vestiges became sclerotized and hard and the place at the base of these vestiges invaginated to better store the spermatozoa.

The remaining phrynichids, however, evolved into another direction. In *Damon*, and convergently in most Phrynichinae, the appendage vestiges were lost.

Some of the western species of *Damon* still have appendage rudiments. In *Damon johnstonii* (Pocock 1894) (Fig. 24) and in *Damon tibialis* (Simon 1876) there is a small appendage rudiment which has, perhaps, a sensory function; nothing is known about spermatophores and sperm transfer in these species.

Another undescribed species from Cameroon has evolved very different genitalia. The gonopods are enlarged hook-like structures which are strongly sclerotized and black (Fig. 25). Again, nothing is known about spermatophores and sperm transfer, but these genitalia strongly suggest that the spermatophores are very different from those of other *Damon* species. This species may be the sister taxon of the Phrynidae, in which case the Phrynichidae form a paraphyletic group. But this is unlikely. The *Damon* species are united by clear synapomorphies, and the genitalia of this *Damon* species and of the Phrynidae are only



Figures 16–21.—Spermatophores of two species of the Phrynidae. 16. Spermatophore of *Heterophrynus longicornis*, lateral view; 17. Anterior view of spermatophore head; 18. Right sperm package enlarged (from Weygoldt 1972b); 19. Spermatophore of *Phrynus marginemaculatus*, anterior view; 20. The same, lateral view; 21. One of the sperm packages enlarged (from Weygoldt 1969). Abbreviations: a = arm-like distal extension, s = spermatozoa, sp = sperm package.

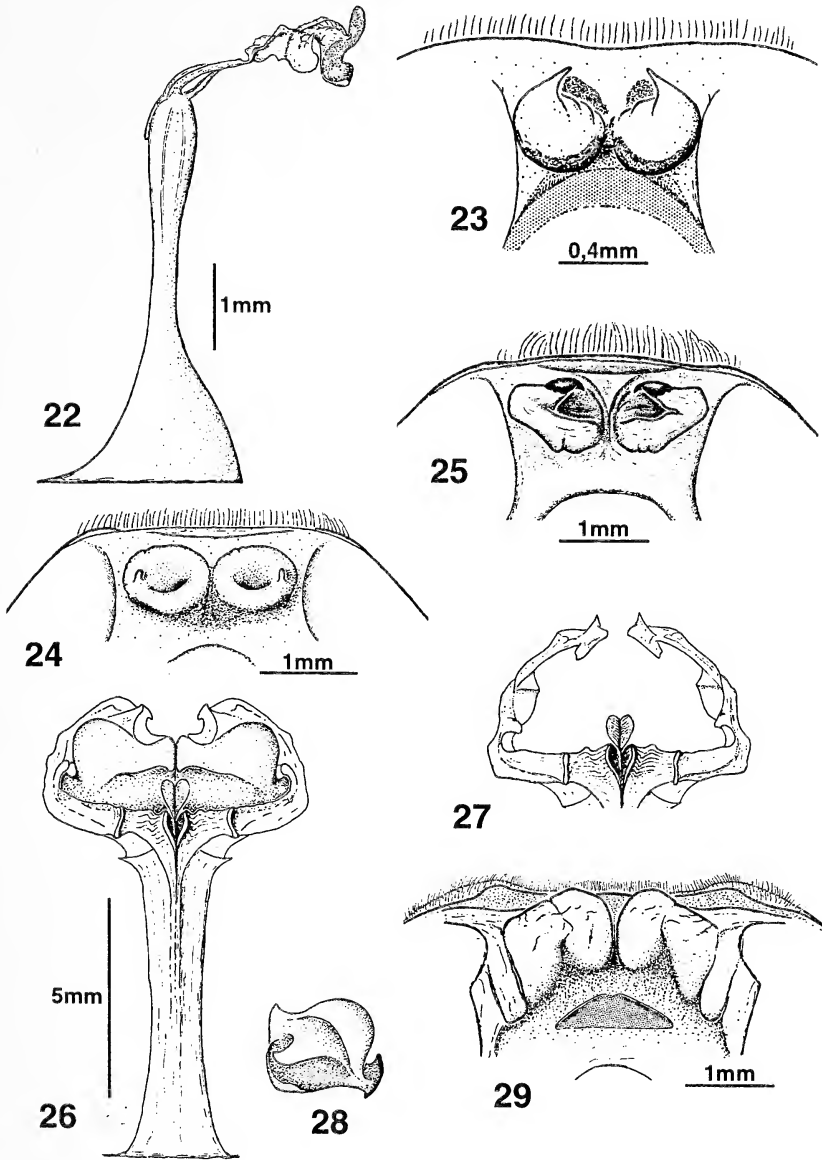
superficially similar. There is no claw-like sclerite on a soft cushion-like gonopod with seminal receptacles, but the tip of the gonopod is sclerotized. It is more likely that this similarity is the result of convergent evolution.

Damon medius (Herbst 1797), another West African species, has its lost gonopodial appendage vestiges. The gonopods are large cushions with a deep dorsal depression. They look more like a depression surrounded by large walls which join in the midline.

In all East African species of *Damon*, the female genitalia are flat cushions without any appendage vestiges. They are supported by an anterior sclerotized plate or bar (Fig. 29).

These cushions are used to detach large sperm-packages from the spermatophore (Weygoldt 1998a; Weygoldt & Hoffmann 1995) (Figs. 26–28). The sperm packages are so large that they fill out nearly the complete genital atrium. This is a specialty of this *Damon variegatus* species group or of all *Damon* species; the reproductive biology of the western species is unknown. The larger parts of these sperm packages consist of a secreted mass which serves perhaps as a matrix to hold and retain the spermatozoa within the female genital atrium; seminal receptacles are missing (Weygoldt & Hoffmann 1995).

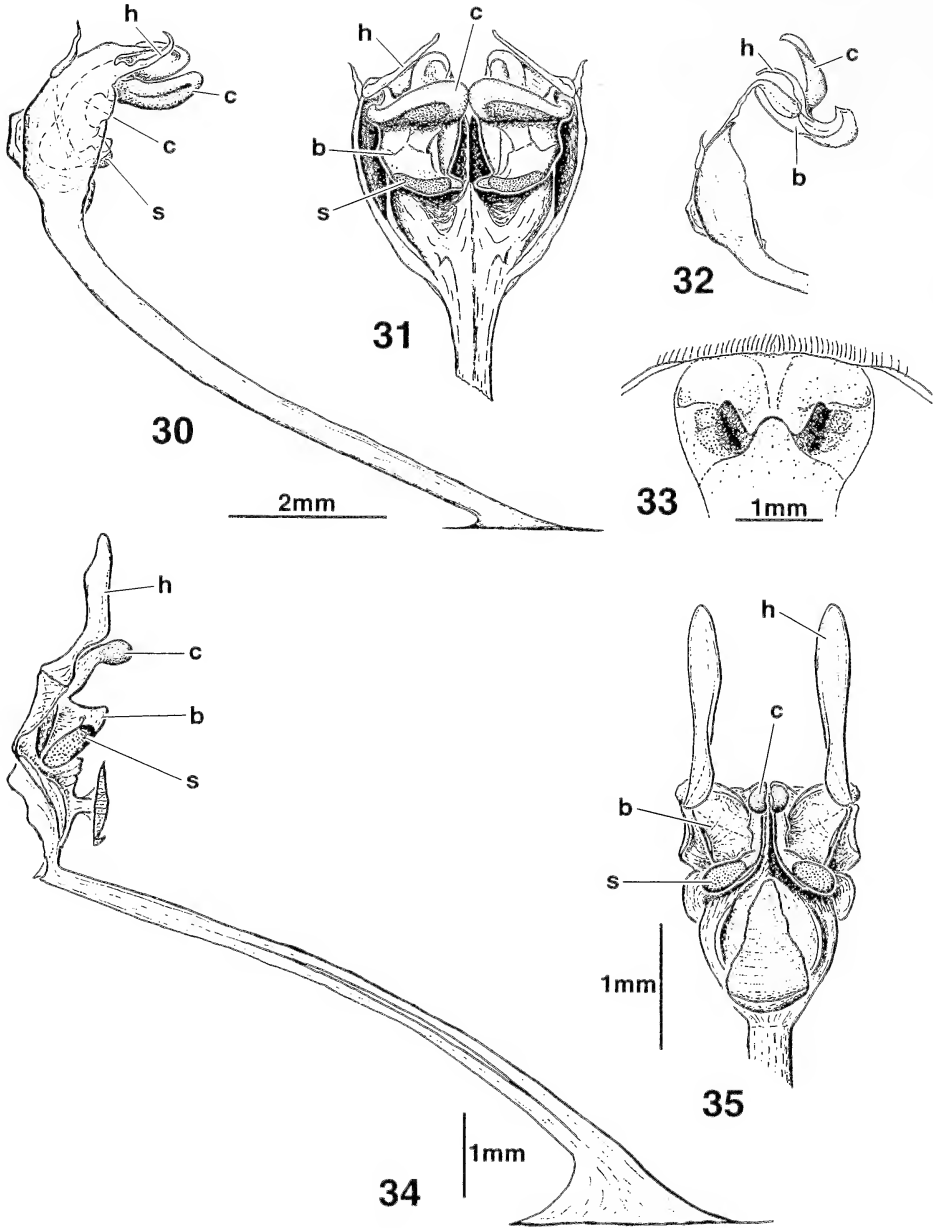
The female genitalia of the Old World



Figures 22–29.—Spermatophores of *Phrynichodamon* and *Damon*. 22. Spermatophore of *Phrynichodamon scullyi*, lateral view (from Weygoldt 1998a); 23. Female genitalia of *Phrynichodamon scullyi*, dorsal aspect (from Weygoldt 1996a); 24. Female genitalia of *Damon johnstonii*, dorsal aspect; 25. Female genitalia of undescribed *Damon* species, dorsal aspect; 26. Spermatophore of *Damon diadema*, anterior view; 27. Anterior view of spermatophore head of emptied spermatophore; 28. One of the sperm packages; 29. Female genitalia of *Damon diadema*, dorsal aspect (from Weygoldt & Hoffmann 1995).

Phrynichinae, the genera *Phrynichus* and *Euphrynichus*, are simple cushion-like elevations which, in some species, have partly sclerotized walls or tooth-like sclerotized tips (Fig. 33). There are no seminal receptacles; the spermatozoa are stored inside the genital atrium. The spermatophores of all Phrynichinae are complex and unique. Their spermatophore

heads consist of an outer frame and two inner bars, each carrying a compact sperm mass at its proximal end (Figs. 30, 31, 34, 35). At the distal end of the spermatophore head there are arms or levers and, at the basis of these, cushions. If these levers or the cushions are pressed down, the bars carrying the sperm masses are elevated (Weygoldt 1998a; Wey-

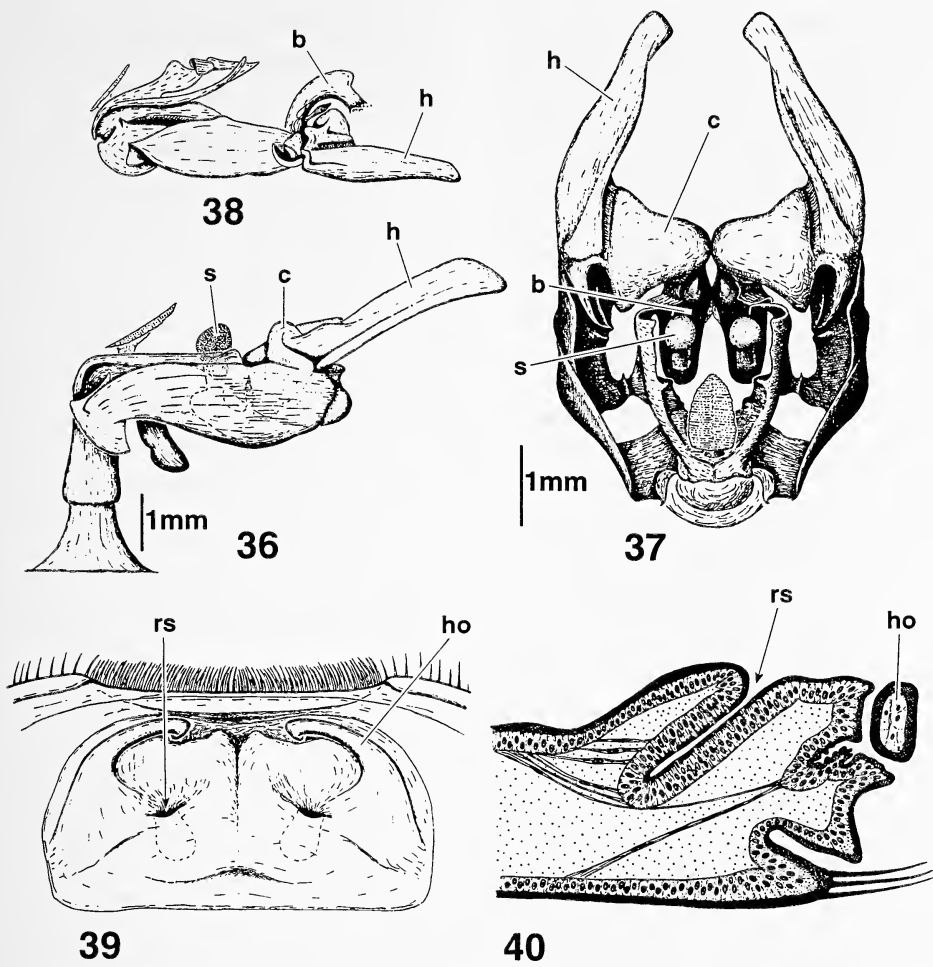


Figures 30–35.—Spermatophores of *Phrynichus* and *Euphrynichus*. 30. Lateral view of total spermatophore of *Phrynichus ceylonicus*, 31. Dorsal aspect of spermatophore head of same; 32. Spermatophore head of emptied spermatophore (from Weygoldt & Hoffmann 1995); 33. Female genitalia of *Phrynichus ceylonicus*, dorsal aspect (from Weygoldt 1998b); 34. Lateral view of total spermatophore of *Euphrynichus bacillifer*; 35. Dorsal aspect of spermatophore head (from Weygoldt 1998a). Abbreviations: b = bar carrying sperm mass, c = cushion, h = lateral horn, s = sperm mass.

goldt & Hoffmann 1995) (Fig. 32) and the sperm masses can be grasped by the female gonopore.

Trichodamon froesi Mello Leitão 1940, a member of the only New World phrynichid

genus, has female genitalia which bear some similarity to those of the Phrynidae (Weygoldt 1977). The gonopods are soft cushions with a hook-like appendage vestige, and close to each hook there is a small seminal receptacle



Figures 36–40.—Spermatophore and female genitalia of *Trichodamon froesi* (from Weygoldt 1977). 36. Lateral view of total spermatophore; 37. Dorsal aspect of spermatophore head; 38. Lateral view of emptied spermatophore head; 39. Female genitalia, dorsal aspect; 40. Longitudinal section through one of the gonopods. Abbreviations: b = bar carrying sperm mass, c = cushion, h = lateral horn, ho = hook-like structure, rs = seminal receptacle, s = sperm mass.

(Figs. 39, 40). The spermatophore of this species is composed of the same parts as those of the Old World Phrynichinae and have the same mechanism, but they are stronger, with a short and stout stalk and a strong outer frame (Figs. 36–38). If the large cushions are pressed down, the bars carrying the sperm masses are lifted and finally arrested (Fig. 38). The hook-like appendage vestiges are probably used to grasp around the bases of the sperm masses and lead them into the seminal receptacles.

DISCUSSION

Courtship behavior is similar in all whip spiders observed; and, although there are

spectacular variations, it will not be discussed here in detail. One of the characteristic features of the Amblypygi is the fact that the male turns away from the female during spermatophore formation. The Amblypygi share this behavior with the Uropygi; in other arachnids which deposit spermatophores, the male faces the female during spermatophore production. This characteristic behavior can be assumed to be synapomorphic either for the Pedipalpi (Uropygi and Amblypygi) or for the Megoperculata (Uropygi, Amblypygi and Araneae). I believe, and Alexander & Ewer (1957) do also, that this latter possibility is the correct one. As a consequence, we have to assume that spiders lost this behavior—per-

haps better, changed this behavior—in the course of the evolution of their characteristic indirect-direct method of sperm transfer. Alexander (1962a, b) was the first to observe mating in amblypygids. She described spermatophore formation as a two step process: The male first deposits an empty spermatophore, then turns to the female again and fills the spermatophore with spermatozoa. Alexander & Ewer (1957) used this two step process to understand the evolution of mating behavior in spiders. In some spiders, the male courts the female for a while, then interrupts courtship in order to fill his palpal copulatory organs. Thereafter he turns toward the female again and resumes courtship. In other species, the filling of the copulatory organs and courtship are two completely separated behavior acts. The behavior of the male whip spider, in which he turns away from the female to produce an empty spermatophore, was hypothesized by Alexander & Ewer (1957) to have been the initial step leading to the reproductive behavior of spiders. However, the observation of Alexander is incorrect. I have now observed and videotaped the behavior of several species of *Damon*, including *D. variegatus*, the same species Alexander observed. In all amblypygid species observed, the spermatozoa are firmly built into the spermatophore as soon as the male lifts his body and starts to turn towards the female again. We can, of course, still assume that a behavior by which the male turns away from the female before spermatophore formation was the initial step from which spider mating behavior evolved.

Male and female genitalia, or spermatophores and female genitalia, have evolved as means to successfully transfer sperm and thus ensure insemination. I assume that they have been shaped by sexual selection in the sense of Eberhard (1985). It is evident from these few examples of Amblypygi that the co-evolution of spermatophores and female genitalia has led to different structures and mechanisms. It is also evident that the structures vary among genera and families and that they can be used as characters in systematic research.

The comparative approach demonstrated here helps to understand the origin and evolution of complex genitalia such as those of *Trichodamon* or of the Phrynidae with their claw-like sclerites and seminal receptacles.

The genitalia also provide useful characters for taxonomy. For example, all Phrynidae are characterized by gonopods with claw-like sclerites and seminal receptacles. Species without this morphological arrangement cannot belong to the family Phrynidae unless it can be shown that the species in question shares other synapomorphies with the Phrynidae and has not yet evolved the typical genitalia, or that it has reduced these structures. Thus, the Namibian *Xerophrynus machadoi* (Purcell 1901) which had been described as *Paraphrynus machadoi*, has female genitalia different from those of all phrynids and, in fact, different from those of all other species. Because of other characters, this species is probably a remote plesiomorphic member of the Phrynichidae (Weygoldt 1996a). Unfortunately, the reproductive biology of this desert-adapted species is not known. In captivity it refuses to produce a spermatophore; perhaps reproductive behavior is triggered by a complex set of environmental changes. Therefore the mechanism of sperm transfer in this species has yet to be discovered.

Genitalia with claw-like sclerites and seminal receptacles are an autapomorphy of the Phrynidae. Quintero (1980) assumed that such claw-like sclerites are an autapomorphy of the Phrynida (Phrynichidae and Phrynidae) and that the Phrynichidae, with the exception of the undescribed *Damon* species, have reduced these sclerites. But this is unlikely. The *Damon* species and the Phrynichinae are united by clear synapomorphies, and the genitalia of this *Damon* species and of the Phrynidae are only superficially similar. It is more likely that this similarity is the result of convergent evolution.

There are many more open questions—in fact, there are more questions than answers. For example, the reproductive biology and the exact systematic position of *Muscodamon atlanteus* Fage 1939 within the Phrynichidae is unknown. This species is known from only four badly-preserved museum specimens.

The situation is even worse in the Charinidae. Although many species have the typical gonopods with a finger-like appendage vestige, some lack them. The Brazilian species of *Charinus* possess sucker-like gonopods, and those of *Charinus seychellarum* are even more different. The spermatophore and female genitalia of this species are unique among ambly-

pygids. The spermatophore resembles those of some pseudoscorpions or whip scorpions (Uropygi). It came as a surprise to find such different spermatophores within one genus, and it is hard to believe that species with such different genitalia should be found in the same genus. The gonopods of *Tricharinus* Quintero 1986 are also different. Quintero (1986) published SEM pictures which reveal similar details to my own unpublished light microscopy studies. The mechanism of these gonopods remain unknown, as the spermatophores are not known; and there are no histological data. The various spermatophores and genitalia in different *Charinus* species and their relatives may suggest that this genus is a paraphyletic or even polyphyletic assemblage, and the fact that the Charinidae as a whole are not characterized by synapomorphies shows that studies of the reproductive biology and the associated structures of these genera are urgently needed and that there is ample work to do for the next generation.

Another unsolved question is the functional significance of various part of the complex spermatophore heads. Perhaps studies with larger numbers of specimens, some of which may produce spermatophores with slight morphological differences, may lead to an understanding of female choice and sexual selection. Sexual selection and sperm competition have never been studied in any whip spider, and the meaning or information content of the different behavior elements during courtship or fighting are completely obscure.

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ONTOGENY OF CHARACTERISTIC LEG MACROSETAE IN *MIMETUS* (ARANEAE, MIMETIDAE)

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ABSTRACT. The distinctive prolateral spination of the metatarsi and tibiae of the first two legs in *Mimetus* is obscure in the first post-eggsac eclosion instar. Only one of the small, acuminate tipped macrosetae appears in the first instar, small macroseta numbers increase in the second instar, and outnumber the large macrosetae by the third instar. The high variability in adult macroseta counts occurs in the third instar as well. The characteristic macrosetae have a socketed base and longitudinally grooved shafts. The large macrosetae are characterized by numbers of small pustules on the base below the emergence of the shaft and the tips of the macrosetae are round. The small macrosetae have fewer pustules or none, and the tips of the macrosetae are falcate and acuminate. Both the large and small macrosetae morphologically resemble presumptive mechano-receptive setae on the legs, and may have a sensory function.

The Mimetidae is a worldwide family of araneophagic spiders, although they will also feed on insect prey captured by other spiders and, rarely, on non-snared insects (Cutler 1972; Jackson & Whitehouse 1986; Lawler 1972). The family is characterized by the distinctive spination of the prolateral surfaces of metatarsi and tibiae of the first two pairs of legs in all females and most males (Forster & Platnick 1984; Heimer 1986; Platnick & Shadab 1993). This spination consists of two different types of macrosetae, referred to as spines by earlier authors. In the adults of *Mimetus*, this spination consists of a series from the distal part of the segment to the proximal part of smaller macrosetae growing smaller in length, followed by a distinctly larger macroseta, another series of small macrosetae decreasing in length, a large macroseta, and so forth with the numbers of series dependent on the leg segment and the species (Fig. 1). Previously, we noted that spiderlings of *Mimetus* emerging from the eggsac lacked the characteristic spination, which provided the impetus for this study.

METHODS

Spiderlings were reared from the first post-eggsac eclosion instar through the third post-

eggsac eclosion instar. Eggsacs were collected in the field and were also produced by females in the laboratory. The eggsacs of *Mimetus notius* Chamberlin 1923 and *M. puritanus* Chamberlin 1923 are morphologically distinctive (Guarisco in press; Guarisco & Mott 1990) and can be readily distinguished.

Specimens of *M. notius* were obtained from Bexar and Medina Counties, Texas and of *M. puritanus* from Douglas County, Kansas. Spiderlings were kept in glass scintillation vials (45 mm tall \times 25 mm diameter) at ambient indoor room temperatures (about 20 °C) and varying light conditions. Food was predominantly first and second instar *Achearanea tepidariorum* (C.L. Koch 1841) (Theridiidae), augmented by first and second instar *Latrodectus mactans* (Fabricius 1775) (Theridiidae), *Argiope aurantia* Lucas 1833 and *Neoscona* sp. (Araneidae), and *Agelenopsis* sp. (Agelenidae).

Two to three days after eggsac emergence (first instar) or after molting (second and third instar) specimens were preserved in 70% ethanol. Samples for scanning electron microscopy (SEM) observations were dehydrated in a graded ethanol series to acetone, air-dried out of acetone, mounted on conductive glue tabs on stubs, sputter coated with 40 nm of

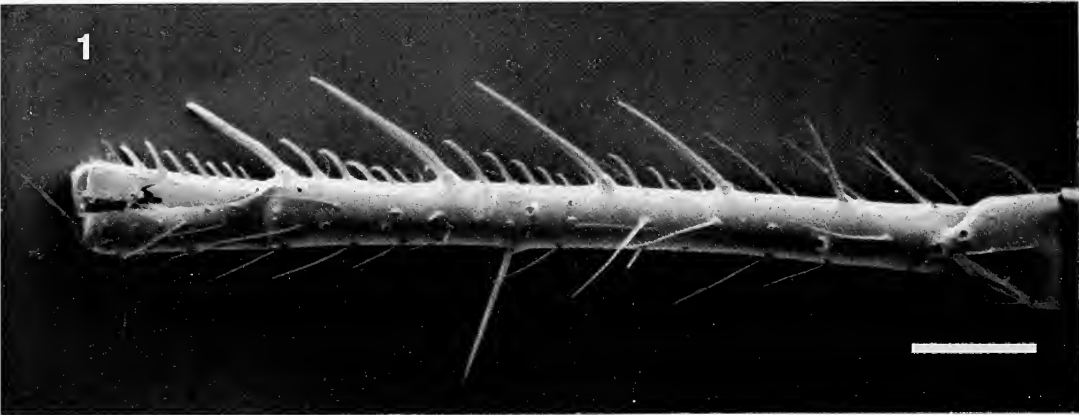


Figure 1.—*Mimetus puritanus*, female from Douglas County, Kansas. Tibia, leg II, top is prolateral, left is distal. Scale bar = 400 μm.

gold: palladium alloy (60:40) and examined by using a Hitachi S570 SEM with a LaB₆ filament. Characteristic spine patterns were determined by examining all specimens available using a dissecting microscope with maximum magnification of 120×. For difficult determinations, specimens were prepared for SEM examination as above. In the tables and text, the smaller macrosetae are indicated by an S, the larger macrosetae by an L, and the order is from distal to proximal.

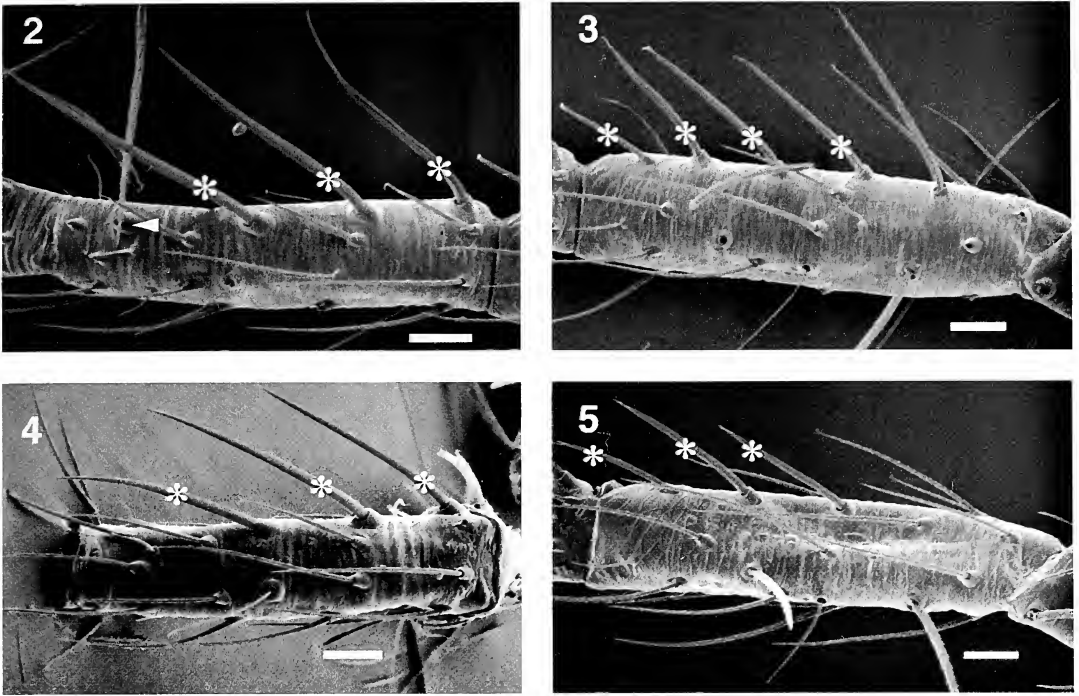
RESULTS

All micrographs are of *Mimetus puritanus*, because of better overall preservation of the material. Unless specified, all macrosetae referred to in this paper are the prolateral macrosetae that form the characteristic spination. As can be seen in Table 1, only one small macroseta was found in the first instar of both species. All of these macrosetae are about the

same length, and there are no interspersed macrosetae of any type. The numbers of these macrosetae did not vary within the species for the specimens examined (Figs. 2–5). In the second instar (Figs. 6–9) the number of large macrosetae outnumbered the number of small macrosetae. There is no variation in pattern in *M. notius*, but some variation in pattern in *M. puritanus* (Table 1). In the third instar one sees for the first time the typical adult macroseta pattern, albeit in a reduced form, and Fig. 10 shows an example. Compared to the earlier instars, the number of small macrosetae increases, the relative lengths of the small macrosetae versus the large macrosetae is that of the adult pattern, and the number of small macrosetae per segment is greater than that of the large macrosetae. A total of seven third instar *M. notius* and five third instar *M. puritanus* was examined. The amount of variability was so great that displaying the information in a

Table 1.—Macroseta types and counts in the two first instars of *Mimetus notius* and *Mimetus puritanus*. Numbers in parentheses are numbers of individuals with a particular macroseta count (if not specifically indicated, the counts are for all *n*); macroseta counts are listed from distal to proximal positions on leg segment. Each specimen had the same spination on right and left corresponding leg segments S = small macroseta, L = large macroseta.

Species	Instar	<i>n</i>	Metatarsus 1	Tibia	Metatarsus 2	Tibia 2
<i>M. notius</i>	first	23	S, 3L	4L	3L	2L
<i>M. notius</i>	second	17	2S, L, S, 2L, S, L	6L	2S, 3L	S, 2L, S
<i>M. puritanus</i>	first	8	S, 3L	4L	3L	3L
<i>M. puritanus</i>	second	9	2S, L, S, 3L	5L(8) Damage(1)	2S, 3L(8) 2S, 2L(1)	S, 2L(4) S, 3L, S(2) S, 2L, S(2) S, L, S, L(1)



Figures 2–5.—*Mimetus puritanus*, first instar from Douglas County, Kansas. Top of image is prolateral, left is distal. 2, Metatarsus I, small macroseta socket indicated by arrowhead, scale bar = 50 μm ; 3, Tibia I, scale bar = 50 μm ; 4, Metatarsus II, scale bar = 40 μm ; 5, Tibia II, scale bar = 40 μm . Asterisks = large macrosetae.

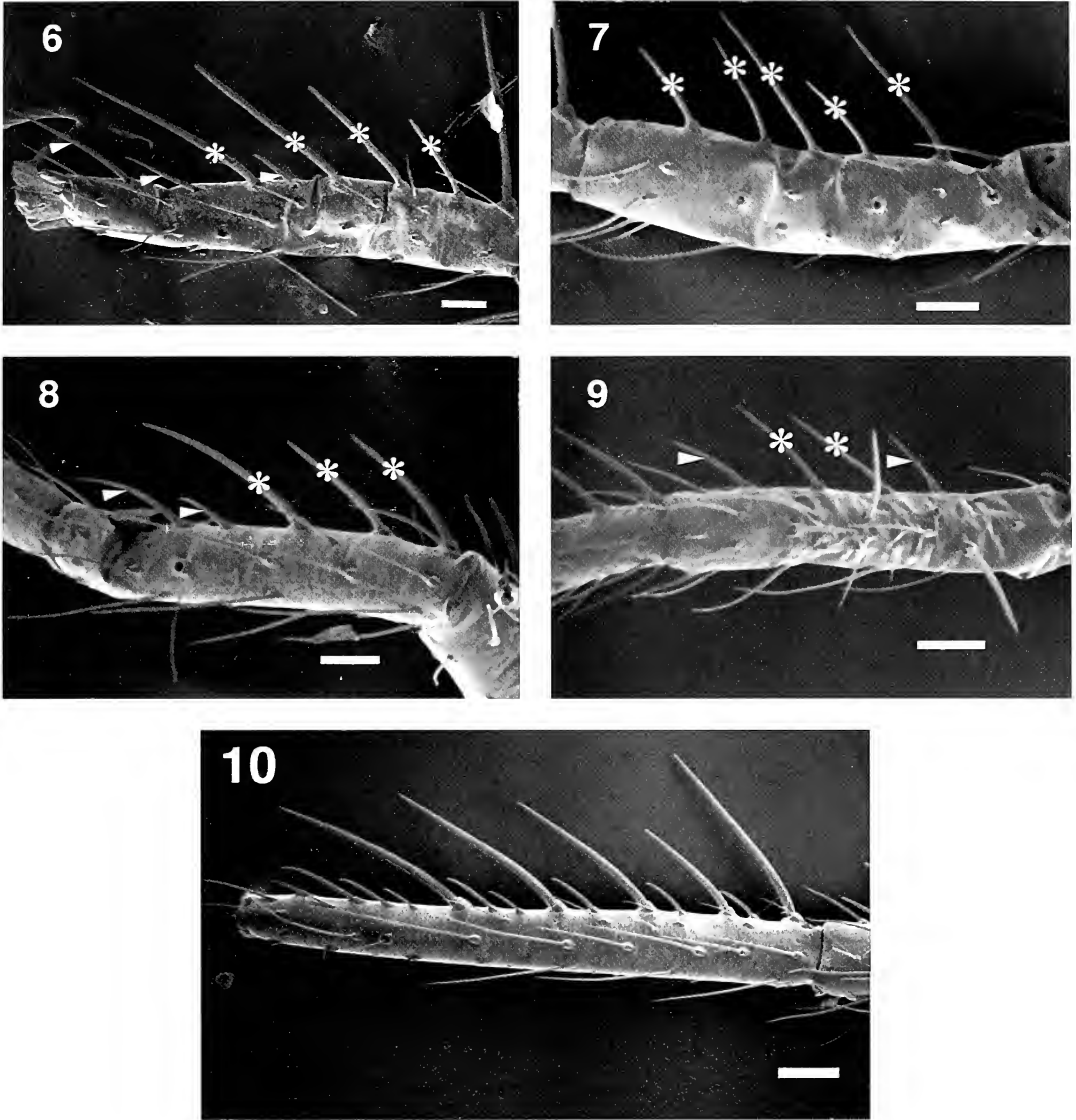
table would be unwieldy. In 32% of the segments examined, the corresponding left and right segments on the same specimen had different macrosetae type counts. As might be expected there were also differences among the individuals.

In all instars examined there are differences in ultrastructural morphology between large and small macroseta of *Mimetus*. The macrosetae emerge from a socket base, both the base and the macroseta shaft have linear ridges, and some of the ridges are hackled (Figs. 11, 12, 15). On the base of the large macrosetae below the emergence of the macroseta shaft there is a large number of approximately 0.5–1.0 μm pustules (Fig. 11). These occur in smaller numbers on the larger of the small macrosetae, but are absent in most of the small macrosetae and the sensory setae on the leg segments (Figs. 12, 15). Another difference between the large macrosetae and the small is that the tips of the large macrosetae are rounded and the macroseta shaft is straight or gently curved, while small macrosetae have falcate, acuminate tips and the macroseta shaft

is strongly curved (Figs. 13, 14). The difference in tip shape becomes more pronounced in the later instars.

DISCUSSION

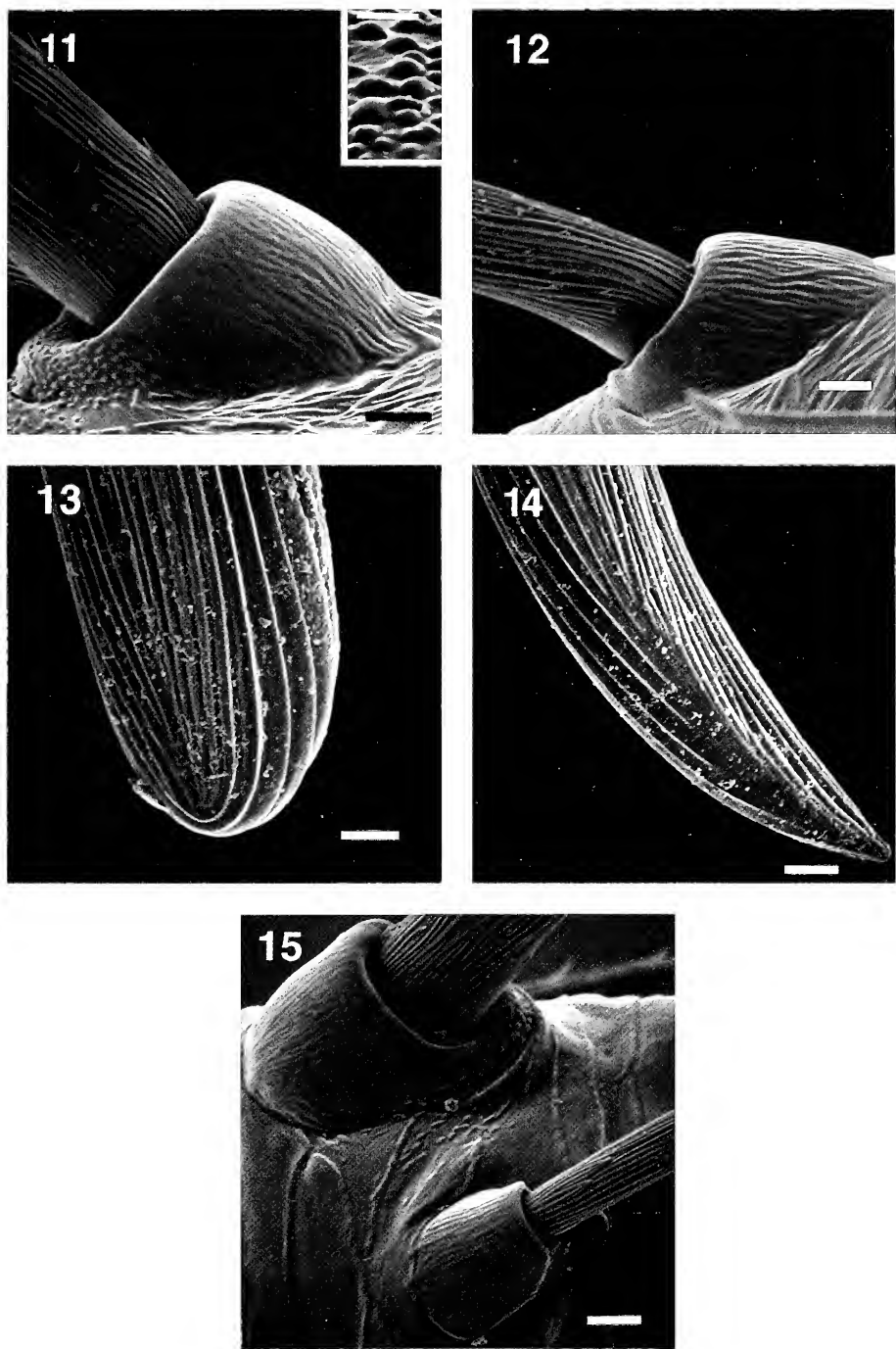
Leg segment macroseta counts in adult *Mimetus* are very variable. Total macroseta counts for Leg I and II metatarsi and tibiae are given in Table 2 (from Mott 1989). The counts are for all macrosetae, not just those that form the characteristic spination. Since the other macrosetae are constant in number, the variation results from the macrosetae making up the characteristic spination. There are no observations, including the most detailed study of mimetid behavior (Jackson & Whitehouse 1986), that indicate a specific function for the macrosetae. Anecdotal observations of the three authors indicate that the macrosetae form a trapping basket in drawing the prey's leg to the chelicerae. They may have a sensory function, since they strongly resemble the smaller presumed, mechano-receptive setae on the legs. These serrate setae are morphologically very similar to the closed tactile



Figures 6–10.—*Mimetus puritanus*, from Douglas County, Kansas. Top of image is prolateral, left is distal. 6–9, Second instar. 6, Metatarsus I, scale bar = 60 μm ; 7, Tibia I, scale bar = 70 μm ; 8, Metatarsus II, scale bar = 60 μm ; 9, Tibia II, scale bar = 80 μm . Asterisks = large macrosetae, arrowheads = small macrosetae; 10, Third instar metatarsus I, macrosetae types obvious, reduced version of adult pattern, scale bar = 90 μm .

setae of *Amaurobius* (reported as *Ciniflo*, Harris & Mill 1977). The shape of the socket bases and the ultrastructure of the shaft is very similar in the setae and macrosetae (Fig. 15). The macrosetae are not simple cuticular projections since they are socketed. Harris & Mill (1977) showed through manipulation that erecting the leg macrosetae in *Amaurobius* cause an electro-physiological response. These macrosetae are morphologically differ-

ent from those of *Mimetus*; however, some sort of tactile response seems a likely function, although probably different from that of *Amaurobius*. The differences in the pustule details and the shape of the macroseta tips provide a way to distinguish the large and small macrosetae in early instars where the discrepancy in the lengths of the macrosetae is much less than in the later instars and adults, and results in difficulty in determining



Figures 11–15.—*Mimetus puritanus*, from Douglas County, Kansas. 11, Base of large macroseta, metatarsus II, third instar, note pustules on base of macroseta socket at lower left, scale bar = 4 μ m, inset, pustules from large macroseta of adult female, scale bar = 1.5 μ m; 12, Base of small macroseta, metatarsus II, third instar, note lack of pustules on macroseta socket base, scale bar = 3.5 μ m; 13, Tip of large macroseta, metatarsus I, adult female, scale bar = 3.5 μ m; 14, Tip of small macroseta, metatarsus I, adult female, scale bar = 3.5 μ m; 15, Large macroseta (top), closed tactile seta (below), metatarsus II, first instar, scale bar = 3.6 μ m.

Table 2.—Total macrosetae per leg segment in adult female *Mimetus notius* (*n* = 10) and *Mimetus puritanus* (*n* = 10). Specimens from eastern United States. S. E. = standard error of the mean (from Mott 1989).

	Meta- tarsus 1	Tibia 1	Meta- tarsus 2	Tibia 2
<i>M. notius</i>				
Range	35–48	31–47	21–30	20–32
Mean	41.9	39.9	26.2	26.4
S. E.	1.760	1.560	1.052	1.046
<i>M. puritanus</i>				
Range	33–53	29–44	21–33	19–29
Mean	40.2	34.5	25.4	23.9
S. E.	2.081	1.614	1.204	1.048

which macroseta type is present. Useful macroseta characteristics in separating the two species occur in the first instar on the second tibia, i.e., there are two large macrosetae in *M. notius* and three in *M. puritanus*. In the second instar there are six large macrosetae on the first tibia in *M. notius*, but only five in *M. puritanus*. Since other species of *Mimetus* occur in the range of the two species discussed here (Mott 1989) and no descriptions of the early instars in these species exist, at this point the macroseta patterns do not have diagnostic value for field collected material. However, once patterns for the early instars of other species becomes available, then these patterns may have diagnostic value.

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VENTRAL MESOSOMAL CHANGES IN EMBRYOS FROM THREE SCORPION FAMILIES: IURIDAE, BUTHIDAE AND VAEJOVIDAE

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ABSTRACT. The scanning electron microscope was used to examine embryos at a stage when booklungs and spiracles are forming. Earlier studies with scorpion fossils suggest there was ventral mesosomal transition from gills or booklungs above ventral plates to sternites, booklungs and spiracles. In *Hadrurus arizonensis* (Iuridae), ventral plates and then sternites are formed on the ventral surface of mesosomal segments before spiracles appear. Bilateral invaginations in body segments XII–XV apparently give rise to the booklungs, with spiracles formed lateral to the site of invagination. Sternites with bilateral depressions were also present before spiracles in embryos of the buthid *Centruroides exilicauda*. In the developmental stages herein examined, spiracles were formed in embryos of *Paruroctonus mesaensis* (Vaejovidae); but there was no indication of ventral plates or sternites on the ventral mesosoma. Spiracles appear in the intersegmental area posterior to body segments XIII–XV. Booklungs may form later from primordia associated with bilateral depressions observed in a later stage in these segments.

The earliest scorpion fossils (Silurian) suggest these animals were aquatic, while all surviving species are terrestrial (Selden & Jeram 1989; Sissom 1990; Jeram 1994). A critical stage in scorpion evolution was the change (ventral mesosoma) from gills to booklungs, probably in the Permian and Carboniferous periods. Kjellesvig-Waering (1986) provided some evidence that aquatic scorpions had gills above ventral plates in the ventral mesosoma. He proposed that there was gradual reduction of these plates and formation of sternites, booklungs and spiracles. Selden & Jeram (1989) and Jeram (1990) described a fossil Carboniferous scorpion with booklungs rather than gills above ventral plates.

Scorpion embryos were examined with the possibility they might provide some information about the water-to-land transition (Farley 1999a, b). These initial observations showed some differences in the ventral mesosoma during spiracle and booklung formation in embryos of the vaejovid, *Paruroctonus mesaensis*, and the iurid, *Hadrurus arizonensis*. The present study is an extension of that work, including embryos of *Centruroides exilicauda*, a buthid. The latter was examined since buthids are considered most primitive among extant scorpion families (Stockwell 1989, 1992; Sissom 1990), and mesosomal changes may reflect the ancestral condition.

METHODS

The composition of physiological saline and the procedures for collection and maintenance of specimens were described in an earlier publication (Farley 1987). Specimens of *Paruroctonus mesaensis* Stahnke 1957 were collected in the Colorado Desert near Indio and Palm Springs, California. Specimens of *Hadrurus arizonensis* Ewing 1928 (Williams 1970; Francke & Soleglad 1981) and *Centruroides exilicauda* Wood 1863a (Wood 1863b; Ewing 1928; Williams 1980) were collected in Arizona. Specimens of all three species are in the California Academy of Science, San Francisco.

Tissues were flushed with saline to remove debris as animals were dissected with microscissors and forceps. The ovariuterine tubules were opened and embryos removed. Surrounding membranes (amnion, serosa) were pulled away with microprobe and forceps.

Tissues were fixed (6–10 h, 23–25 °C) with 4% glutaraldehyde in 0.1 M cacodylate buffer with one drop of calcium chloride for each 10 ml of solution (Lane et al. 1981). The tissues were washed in cacodylate buffer-NaCl solution and postfixed (2 h, 23–25 °C) in 1% osmium tetroxide in 0.2 M cacodylate buffer with NaCl. The concentrations of these solutions were adjusted to approximate the os-

molality of scorpion blood (630 mOsm; Yokota 1984). Tissues were dehydrated in acetone, critically-point dried (Balzers, CDD 020) and sputter-coated (EMscope SC500) with 20 nm thickness of gold/palladium. Tissues were examined at 12–15 KV with a Philips 15 scanning electron microscope (SEM).

RESULTS

At a stage before spiracle and booklung formation, embryos of *H. arizonensis* have plates demarcated on the ventral surface of mesosomal segments. Initially, only a narrow ridge outlines the ventral plates, with the delineated region much smaller than the ventral surface of the segment. The outlined region becomes a flap-like structure (Fig. 1) fused to the body wall anteriorly but free at the lateral and posterior margins. The early ventral plates do not extend the full width of the mesosoma nor overlap antero-posteriorly. Embryos were not sectioned, but no indications of an opening or gill-like structures were observed at the posterior margin of the ventral plates. Paired indentations in body segments XII–XV (Hjelle 1990) are presumably booklung primordia.

In later stages, the invaginations in segments XII–XV become more prominent (Fig. 2), and the ventral cuticle increases in length and width, forming structures that resemble adult sternites with the perimeter joined to pleural or intersegmental integument. The sternites extend the full width of the mesosoma and overlap in the longitudinal axis. Intrasternal spiracles eventually form at the adult location (Farley 1990a, b), just lateral to the site of booklung invagination. Booklungs do not develop in segment XVI; the indentations (Fig. 2) eventually disappear, leaving no external trace. Mesosomal development in the buthid, *C. exilicauda*, appears to be similar to that of *H. arizonensis*. In Fig. 3, an embryo of the former species has sternites with bilateral depressions, presumably for booklungs.

In embryos of *P. mesaensis*, there is no demarcation of ventral plates or sternites at the time when spiracles first appear (Fig. 4). In the stages observed in this study, spiracles were seen near the mesosomal midline in the intersegmental tissue posterior to segments XIII–XV. In later stages, bilateral depressions were seen in segments XII–XVI, but there was still no indication of ventral plates or sternites. Advanced embryos of *P. mesaensis* were not

available to determine if booklungs and new spiracles form at these depression sites, or if the initial spiracles (Fig. 4) move to the adult position, farther anterior and lateral in the segment (Farley 1990a, b). The early spiracles differed in shape among the embryos, but usually had a smooth, apparently cuticular margin and a slit-like opening (Fig. 4), in comparison with the oval shape in the adult.

Although ventral plates or sternites are not evident in embryos of *P. mesaensis* when spiracles first appear (Fig. 4), the ventro-posterior margin of each mesosomal segment was examined for indications of invagination or gill-like structures. In some embryos, the lateral intersegmental area shows differentiation suggestive of infolding, with vertical striations (Fig. 4). The spiracles form in the medial aspect of this distinctive intersegmental area.

Embryos were not sectioned, but during dissection in transmitted light, some internal structures can be seen. In embryos of *P. mesaensis*, there was no indication of a thickening or density anterior to the spiracles, as would be expected if booklungs were forming. The spiracle site in the intersegmental area (Fig. 4) did not appear to be a region of invagination as occurs in the bilateral depressions seen in the mesosomal segments of the iurid and buthid embryos (Figs. 1–3).

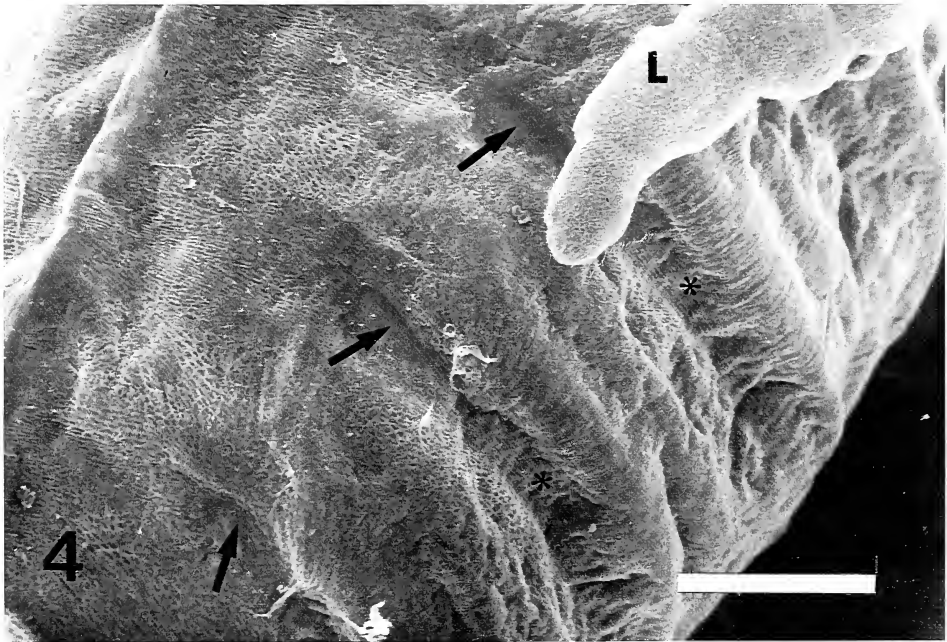
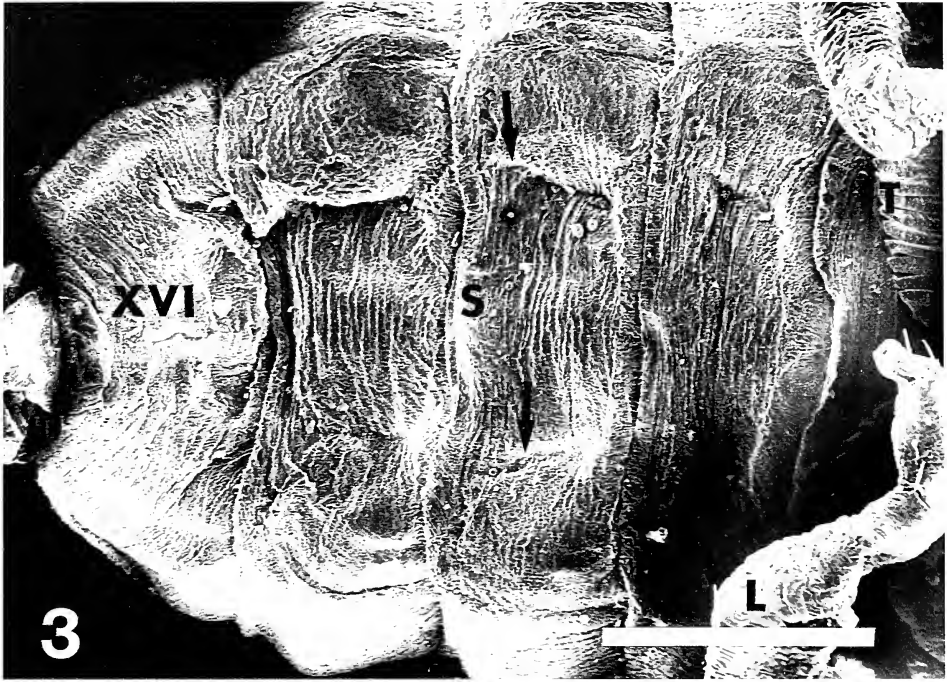
DISCUSSION

In *H. arizonensis* and *C. exilicauda*, booklung and spiracle formation appears to be like that described by earlier workers in species from the families Buthidae (Abd-el Wahab 1951), Chactidae (Laurie 1890; Brauer 1895) and Scorpionidae (Metschnikoff 1871; Laurie 1892). The bilateral depressions evident in mesosomal segments in Figs. 1–3 appear to be sites of invagination, and spiracles are later formed here at the location seen in adults (Farley 1990a, b). The early demarcation of flap-like structures (Fig. 1) supports the notion that ventral plates preceded (Kjellesvig-Waering 1986) or occurred with booklungs in ancient scorpions (Selden & Jeram 1989; Jeram 1990).

Differences were reported among scorpion species in the shape and texture of the cuticle of adult booklung lamellae (Lankester 1885; Berteaux 1889; Laurie 1896a, b). These were proposed as taxonomic criteria, but other features subsequently found acceptance (Stock-



Figures 1, 2.—SEMs of ventral surface of mesosoma of embryos of *Hadrurus arizonensis*. 1. Flap-like ventral plates (P) are fused to the body wall anteriorly and free at the posterior margin. Bilateral invaginations (arrows) are present where spiracles and booklungs will eventually form. Teeth (T) are evident at the posterior edge of the pectines. XIV, body segment; 2, Later stage. The ventral cuticle of each segment has broadened and is now a sternite (S) attached around the entire perimeter. Bilateral invaginations (black arrows) have deepened. Shallow depressions occur in body segment XVI, but booklungs do not develop in this segment. The white arrow indicates a pair of small, transitory appendages of unknown significance between gonopore and pectine. A, remnants of amnion not removed during preparation; T, pectinal teeth. Scales, 0.5 mm.



Figures 3, 4.—SEMs of ventral surface of mesosoma of embryos. 3, *Centruroides exilicauda*. Each segment has a sternite (S) like that of the irurid embryo of Figure 2. Bilateral invaginations (arrows) are presumably the site of booklung formation. Depressions are evident in body segment XVI although booklungs do not form in this segment. L, fourth walking leg. T, pectinal teeth. Scale, 0.5 mm; 4, *Paruroctonus mesaensis*, left side of ventral mesosoma. No ventral plates or sternites are evident, but spiracles (arrows) are present at the posterior margin of body segments XIII–XV. The spiracles are at the medial end of an invaginated intersegmental region (*) with vertical striations. L, fourth walking leg. Scale, 0.2 mm.

well, 1989, 1992; Sissom 1990). Developing booklungs were previously described as bilateral invaginations in the ventral mesosoma (Metschnikoff 1871; Laurie 1890, 1892; Brauer 1895; Abd-el Wahab 1951). Tissue sections showed that sac-like invaginations extend anteriorly in the segment from the initial site of ingress, which remains open to become the spiracle. A few lamellae are initially formed in the horizontal plane. These later rotate 90° to the dorso-ventral axis, along with development of many more lamellae (Laurie 1890, 1892).

There may be absence or delay of ventral plates, and sternites may form late in embryos of *P. mesaensis* in comparison with the iurid and buthid embryos. Among scorpion families, heterochrony occurs in embryogenesis in relation to the mode of maternal nourishment of the embryos (Matthew 1959; Farley 1999a, b). All extant scorpions have adaptations for terrestrialization (*i.e.*, oral tube, booklungs, latterly compressed podomeres), but may be polyphyletic with convergent evolution (Jeram 1994). The possibility of a different vaejovid derivation is raised in the present studies by the delay or absence of ventral plates (Fig. 4) and the development of spiracles at the medial end of lateral intersegmental specializations that may be indicative of ancestral respiratory structures. Fossils of British Triassic scorpions have slit-like spiracles in the intersegmental membrane of mesosomal segments or in the latero-posterior margin of the abdominal plates (Wills 1947).

Tissue sections are needed to determine if booklung formation is also distinctive in *P. mesaensis*. The lack of tissue invagination at the place where spiracles first appear in the intersegmental area (Fig. 4) suggests this is not the site of booklung primordia. These spiracles may migrate from the intersegmental area to the adult position more anterior and lateral in the segment (Farley 1990a, b). Another possibility is that the early spiracles in Fig. 4 are transitory, and new spiracles form later with booklungs more anterior in the segments.

Kjellesvig-Waering (1986) proposed that ventral plates were abdominal flaps or appendages that overlay the body wall beneath, and sternites developed as the abdominal plates were reduced and eventually lost. From their review of fossil evidence, Selden & Jer-

am (1989) considered it more likely that ventral plates later became sternites by fusion with the body wall. The latter proposal is supported in the present study in embryos of *H. arizonensis*. Small regions, initially outlined by a ridge on the ventral surface of mesosomal segments, become flap-like plates (Fig. 1) and then the ventral cuticle is broadened to form sternites (Fig. 2). There was no indication of reduction or loss of the ventral plates, resulting in exposure of overlying sternites.

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THE USE OF MORPHOMETRIC CHARACTERISTICS FOR THE RECOGNITION OF SPECIES AMONG GONIOSOMATINE HARVESTMEN (ARACHNIDA, OPILIONES, GONYLEPTIDAE)

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ABSTRACT. Morphometric data from males of six species of *Goniosoma* are presented and their importance in characterization and recognition of the species is discussed. Data presented show that it is important to use intraspecific variation during descriptions of these harvestmen.

Harvestmen (Arachnida, Opiliones) are worldwide in distribution. Most papers on harvestmen treat taxonomic aspects. Biological, ecological and behavioral surveys are somewhat rare, especially those dealing with developmental characterization. Most taxonomic papers that describe species present single measurements of body structures. This is, in part, because many species are known by only a single specimen. As discussed by McGhee (1977), the structures may vary among specimens of different populations or even of the same population. Gnaspini (1995) also showed that measurements vary due to developmental differences. In the present paper, variation among different species is analyzed and discussed. The main goal of this paper is to show the importance of taking into account these aspects when diagnosing and describing species of harvestmen. Toward this goal, the morphometric characterization of adults of six different species of *Goniosoma* is presented and discussed.

METHODS

The species treated here were collected during a study focusing on the cavernicolous species *Goniosoma spelaeum* (Mello-Leitão 1933) in the Ribeira Valley, São Paulo State, southeastern Brazil (Gnaspini 1993). The species included in this study were collected in caves in São Paulo State and/or in the neighborhood of the study area, as follows: *Goniosoma* sp. 1 aff. *badium* - caves near Curitiba, Paraná State; *Goniosoma* sp. 2 aff. *badium* - Guaricana Dam, near Curitiba, Paraná State; *Goniosoma longipes* (Roewer 1931) - Caves

near Ipeúna, São Paulo State; *Goniosoma proximum* (Mello-Leitão 1933) - forest in the Ribeira Valley (except when in two specific caves within the distribution of *G. spelaeum* - see Gnaspini 1996), São Paulo State; *Goniosoma spelaeum* (Mello-Leitão 1933) - caves in the Ribeira Valley, São Paulo State; *Goniosoma varium* Perty 1833 - forest and inside the first 0.5 m of caves in the Ribeira Valley, São Paulo State.

Collected animals were fixed in 40% ethyl alcohol and, after some hours, transferred to flasks with 70% alcohol. This procedure avoided hardening of the specimens, especially their leg articulations, and facilitated easy measurements. A series of voucher specimens of all species treated herein is deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP).

Morphometrical and meristic characteristics were observed with a Wild M5A stereomicroscope. The characteristics used in the analysis were the number of tarsal segments and the measurement of body width (maximum width of dorsal scutum), body length (length of the dorsal scutum), total length of the pedipalp and of the walking legs.

The raw data have been statistically analyzed using the Möls' method (Möls 1987 *apud* Neet 1993; Gnaspini 1995), which tests if two given sets have their values homogeneous or heterogeneous, i.e., if they should be considered the same or different from each other. Neet (1993) provided an example of use with spiders and an algorithm for the test. Briefly described, the test first orders the values analyzed and then groups them by values

Table 1.—Results of the Möls's test for each pair of species studied, for body length measurements taken in adult males of *Goniosoma*. “+” = “securely heterogeneous” ($\alpha < 0.01$), “±” = “probably heterogeneous” ($0.01 < \alpha < 0.05$), “-” = “possibly homogeneous” ($\alpha > 0.05$). The value of α is given between parentheses following the respective symbol.

	<i>G. varium</i> (<i>n</i> = 4)	<i>G. spelaeum</i> (<i>n</i> = 8)	<i>G. proximum</i> (<i>n</i> = 10)	<i>G. longipes</i> (<i>n</i> = 5)	<i>G. sp. 2</i> aff. <i>badium</i> (<i>n</i> = 8)
<i>G. sp. 1</i> aff. <i>badium</i> (<i>n</i> = 8)	-(2.13)	-(0.685)	-(0.575)	±(0.041)	-(1.46)
<i>G. sp. 2</i> aff. <i>badium</i>	-(2.78)	-(1.05)	+(0.002)	-(0.317)	
<i>G. longipes</i>	-(0.709)	-(0.167)	-(2.31)		
<i>G. proximum</i>	-(0.079)	-(0.105)			
<i>G. spelaeum</i>	-(3.23)				

as if to prepare a graph of distribution. Following this the data are treated as two curves of distribution that may overlap. The percentage of overlap is represented by α . If α is smaller than 5%, the test considers the distribution heterogeneous, and provides a limit value. Individuals with values smaller than this limit are considered as part of a group, and those with larger values are part of a second group. A series of these pair-wise comparisons then determines the similarities of species.

RESULTS

The number of tarsal segments showed mostly the same ranges among the species studied (global range of 8–12 segments in Leg I, 14–25 in Leg II, 9–14 in leg III, and 9–15 in leg IV), although *G. spelaeum* showed the larger values and *G. varium* showed the smaller values. Because the variation was not statistically significant, the number of tarsal segments proved not to be useful in the recognition among species.

Möls' test of body width measurements

showed that this feature is not also useful in distinguishing the species. The resulting α ranged from 0.154 to 27.55. Figure 1 shows large overlaps among the measurements of the species.

On the other hand, Möls' analyses (Tables 1–6) showed that body length, the length of legs I–IV, and palpal length are useful measurements in distinguishing *Goniosoma* species. Figure 1 shows graphically the differences in the means and variances of these measurements. However, the lengths of body and of palp are useful only for given pairs of species. For example, from Table 6 (palpal length), α (interval of significance of the test) is mostly larger than 5% for the pairs of species analyzed, being coded as a “-” in the table. This means that the differences are not statistically significant. For pair *G. spelaeum* - *G. longipes*, α is smaller than 5%, being statistically significant, and coded as a “±” in the table. Finally, α is smaller than 1%, being coded as a “+” in the table, showing that the differences are highly significant for

Table 2.—Results of the Möls's test for each pair of species studied, for leg I length measurements taken in adult males of *Goniosoma*. “+” = “securely heterogeneous” ($\alpha < 0.01$), “±” = “probably heterogeneous” ($0.01 < \alpha < 0.05$), “-” = “possibly homogeneous” ($\alpha > 0.05$). The value of α is given between parentheses following the respective symbol.

	<i>G. varium</i> (<i>n</i> = 4)	<i>G. spelaeum</i> (<i>n</i> = 8)	<i>G. proximum</i> (<i>n</i> = 10)	<i>G. longipes</i> (<i>n</i> = 5)	<i>G. sp. 2</i> aff. <i>badium</i> (<i>n</i> = 8)
<i>G. sp. 1</i> aff. <i>badium</i> (<i>n</i> = 8)	+(0.0002)	±(0.018)	+(0.0008)	+(0.0015)	+(0.007)
<i>G. sp. 2</i> aff. <i>badium</i>	+(0.0018)	-(19.18)	-(44.68)	+(0.0048)	
<i>G. longipes</i>	-(0.407)	+(0.0012)	+(0.00002)		
<i>G. proximum</i>	+(0.000007)	-(2.76)			
<i>G. spelaeum</i>	+(0.0008)				

Table 3.—Results of the Möls’s test for each pair of species studied, for leg II length measurements taken in adult males of *Goniosoma*. “+” = “securely heterogeneous” ($\alpha < 0.01$), “±” = “probably heterogeneous” ($0.01 < \alpha < 0.05$), “−” = “possibly homogeneous” ($\alpha > 0.05$). The value of α is given between parentheses following the respective symbol.

	<i>G. varium</i> (n = 4)	<i>G. spelaeum</i> (n = 8)	<i>G. proximum</i> (n = 10)	<i>G. longipes</i> (n = 5)	<i>G. sp. 2</i> aff. <i>badium</i> (n = 8)
<i>G. sp. 1</i> aff. <i>badium</i> (n = 8)	±(0.037)	−(0.075)	+(0.0000004)	+(0.0007)	±(0.019)
<i>G. sp. 2</i> aff. <i>badium</i>	−(0.059)	−(8.38)	−(4.08)	+(0.0036)	
<i>G. longipes</i>	−(1.12)	+(0.0069)	+(0.000001)		
<i>G. proximum</i>	+(0.00002)	−(0.134)			
<i>G. spelaeum</i>	±(0.054)				

pairs *G. proximum* - *G. sp. 2* aff. *badium*, *G. proximum* - *G. spelaeum*, and *G. spelaeum* - *G. varium*.

When values of length of legs I, II, III and IV do not allow recognition, other structures can be used. One good example is the case of *G. sp. 2* aff. *badium* and *G. proximum*, which can be easily distinguished by the length of the body and especially of the palp.

The only two pairs of species which could not be statistically recognized using morphometrics were *G. sp. 2* aff. *badium* and *G. spelaeum*, and *G. longipes* and *G. varium*. Therefore, other characters should be used, such as color, as treated below.

DISCUSSION

These data show that there are morphometric, morphological and meristic variations between and within species of harvestmen, as previously discussed by McGhee (1977) and Gnaspini (1995). These intraspecific variations may be even very large, and may be due either to variation within the same developmental stage or between stages. In addition,

adding measurements of single specimens during descriptions (even when series are available) does not allow precise species recognition. For instance, if a given specimen of the same species is checked against measurements of only one described specimen, it may not fit, and would not be recognized as such species. However, if a range of variation was given, it would probably fit.

In addition, data also show that the range of variation may help identify species. Of course, genitalia characterization and color patterns can also help distinguish species from each other. Sometimes, they do so alone; however, in other cases they are conservative and misleading.

In her unpublished revision of the genus *Goniosoma*, Stefanini- Jim (1985, 1995, pers. comm.) proposed synonymizing several species under *G. badium*, due to the conservative shape of their penis. She also considers *G. spelaeum* to belong in a 'badium-group', and possibly being synonymous with *G. badium*, again because of the similar penis. She

Table 4.—Results of the Möls’s test for each pair of species studied, for leg III length measurements taken in adult males of *Goniosoma*. “+” = “securely heterogeneous” ($\alpha < 0.01$), “±” = “probably heterogeneous” ($0.01 < \alpha < 0.05$), “−” = “possibly homogeneous” ($\alpha > 0.05$). The value of α is given between parentheses following the respective symbol.

	<i>G. varium</i> (n = 4)	<i>G. spelaeum</i> (n = 8)	<i>G. proximum</i> (n = 10)	<i>G. longipes</i> (n = 5)	<i>G. sp. 2</i> aff. <i>badium</i> (n = 8)
<i>G. sp. 1</i> aff. <i>badium</i> (n = 8)	+(0.0052)	±(0.011)	+(0.0003)	−(0.069)	+(0.0027)
<i>G. sp. 2</i> aff. <i>badium</i>	+(0.0072)	−(30.80)	−(99.45)	±(0.018)	
<i>G. longipes</i>	−(0.149)	+(0.0041)	+(0.0002)		
<i>G. proximum</i>	+(0.00004)	−(4.37)			
<i>G. spelaeum</i>	+(0.0015)				

Table 5.—Results of the Möls’s test for each pair of species studied, for leg IV length measurements taken in adult males of *Goniosoma*. “+” = “securely heterogeneous” ($\alpha < 0.01$), “±” = “probably heterogeneous” ($0.01 < \alpha < 0.05$), “-” = “possibly homogeneous” ($\alpha > 0.05$). The value of α is given between parentheses following the respective symbol.

	<i>G. varium</i> (n = 4)	<i>G. spelaenum</i> (n = 8)	<i>G. proximum</i> (n = 10)	<i>G. longipes</i> (n = 5)	<i>G. sp. 2</i> <i>aff. badium</i> (n = 8)
<i>G. sp. 1 aff. badium</i> (n = 8)	+(0.0003)	±(0.038)	+(0.0008)	±(0.023)	+(0.0001)
<i>G. sp. 2 aff. badium</i>	+(0.0002)	-(1.06)	-(3.35)	+(0.0025)	
<i>G. longipes</i>	-(0.716)	+(0.0038)	+(0.0002)		
<i>G. proximum</i>	+(0.00002)	±(0.014)			
<i>G. spelaenum</i>	+(0.0007)				

also identified the two species, treated herein as *G. sp. 1* and *2 aff. badium*, as belonging to *G. badium*. However, the morphometric data available showed that these species can be separated. Moreover, they differ in color, both in nature and preserved specimens. *Goniosoma spelaenum* and *G. badium* (*sensu* Stefanini-Jim) are yellowish-brown (however, the latter has very contrasting dark brown legs), whereas the others are darker - *G. sp. 2 aff. badium* being dark brown, and *G. sp. 1 aff. badium* being dark greenish-brown. *Goniosoma sp. 2 aff. badium* has the pleura of articulations between coxae and trochanters pink-colored, whereas the others are white. In addition, this species and *G. badium* (*sensu* Stefanini-Jim) have a series of internal spines on femur IV from base to the medial portion, whereas the others have from one to three medial internal spines on femur IV.

In conclusion, this paper is intended to show that morphometrical variation is important when describing harvestmen and can provide useful information and avoid misidentification of species. Therefore, although

it would take a long time to be done, I suggest that systematists include ranges of variation in their descriptions of new species. These would give a holistic understanding of the species being described, and a larger number of characters to be used in species recognition.

ACKNOWLEDGMENTS

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Table 6.—Results of the Möls’s test for each pair of species studied, for palp length measurements taken in adult males of *Goniosoma*. “+” = “securely heterogeneous” ($\alpha < 0.01$), “±” = “probably heterogeneous” ($0.01 < \alpha < 0.05$), “-” = “possibly homogeneous” ($\alpha > 0.05$). The value of α is given between parentheses following the respective symbol.

	<i>G. varium</i> (n = 4)	<i>G. spelaenum</i> (n = 8)	<i>G. proximum</i> (n = 10)	<i>G. longipes</i> (n = 5)	<i>G. sp. 2</i> <i>aff. badium</i> (n = 8)
<i>G. sp. 1 aff. badium</i> (n = 8)	-(0.144)	-(0.078)	-(1.56)	-(1.30)	-(2.07)
<i>G. sp. 2 aff. badium</i>	-(0.076)	-(2.12)	+(0.0007)	-(1.05)	
<i>G. longipes</i>	-(0.115)	±(0.042)	-(5.56)		
<i>G. proximum</i>	-(0.938)	+(0.000004)			
<i>G. spelaenum</i>	+(0.0050)				

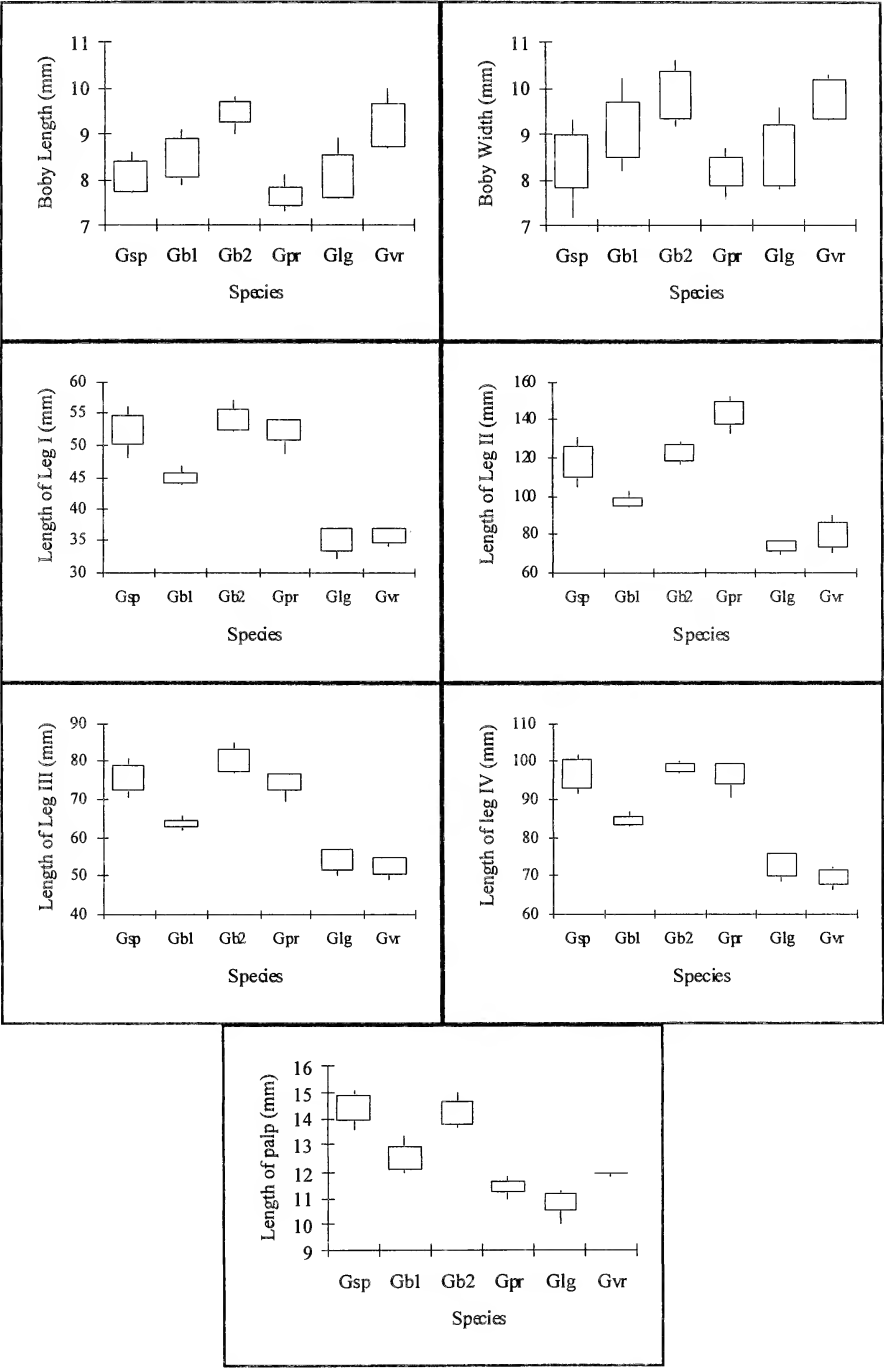


Figure 1.—Mean \pm standard deviation (rectangles) and amplitude of variation (lines) for the morphometric measurements taken in adult males of *Goniosoma spelaeum* (*Gsp*, $n = 8$), *G. sp. 1 aff. badium* (*Gbl*, $n = 8$), *G. sp. 2 aff. badium* (*Gb2*, $n = 5$), *G. proximum* (*Gpr*, $n = 10$), *G. longipes* (*Glg*, $n = 5$), and *G. varium* (*Gvr*, $n = 4$). Values are in millimeters.

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SEXUAL SELECTION IN PHOLCID SPIDERS (ARANEAE, PHOLCIDAE): ARTFUL CHELICERAE AND FORCEFUL GENITALIA

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ABSTRACT. Two aspects of pholcid reproductive biology are reviewed and appear best explained by sexual selection by female choice: the rapid and divergent evolution of male chelicerae (and clypei in some groups) which contact the female epigynum during copulation and probably act as copulatory courtship devices; and the often exceptionally strong pedipalps in males, which possibly function in correlation with the ‘valve’ in the internal female genitalia.

The last decades have seen a promising increase of studies examining spider reproduction from an evolutionary perspective (review: Elgar 1998). In most cases, the mechanisms of sexual selection in spiders are much the same as those documented in insects and other major groups (see e.g., Eberhard 1996, where almost every spider example used to document a specific mechanism of cryptic female choice is accompanied by at least one insect or mammal example). Some details, however, make spiders either especially useful (e.g., the pairedness of genitalia for studies of fluctuating asymmetry - Huber 1996b), or especially interesting (e.g., the apparent lack of both muscles and nerves in the male intromittent genitalia - Eberhard & Huber 1998). (For further, though less unique, spider characteristics, see Elgar 1998.)

In the present paper I will briefly review some recent advances in one particular spider family, the pholcids. Pholcids are the only non-entelegyne spiders whose reproductive biology has been carefully studied in several species (Eberhard 1992; Eberhard & Briceño 1983, 1985; Huber 1994, 1995, 1996a, b, 1997a, b, 1998a, b, c; Huber & Eberhard 1997; Kaster & Jakob 1997; Uhl 1993, 1994; Uhl et al. 1995; Yoward 1998). Further advantages for the study of sexual selection are the number of synanthropic species that are available worldwide and readily maintained in the laboratory for in depth single-species studies, and a rich and diverse (mainly tropical) fauna for comparative studies.

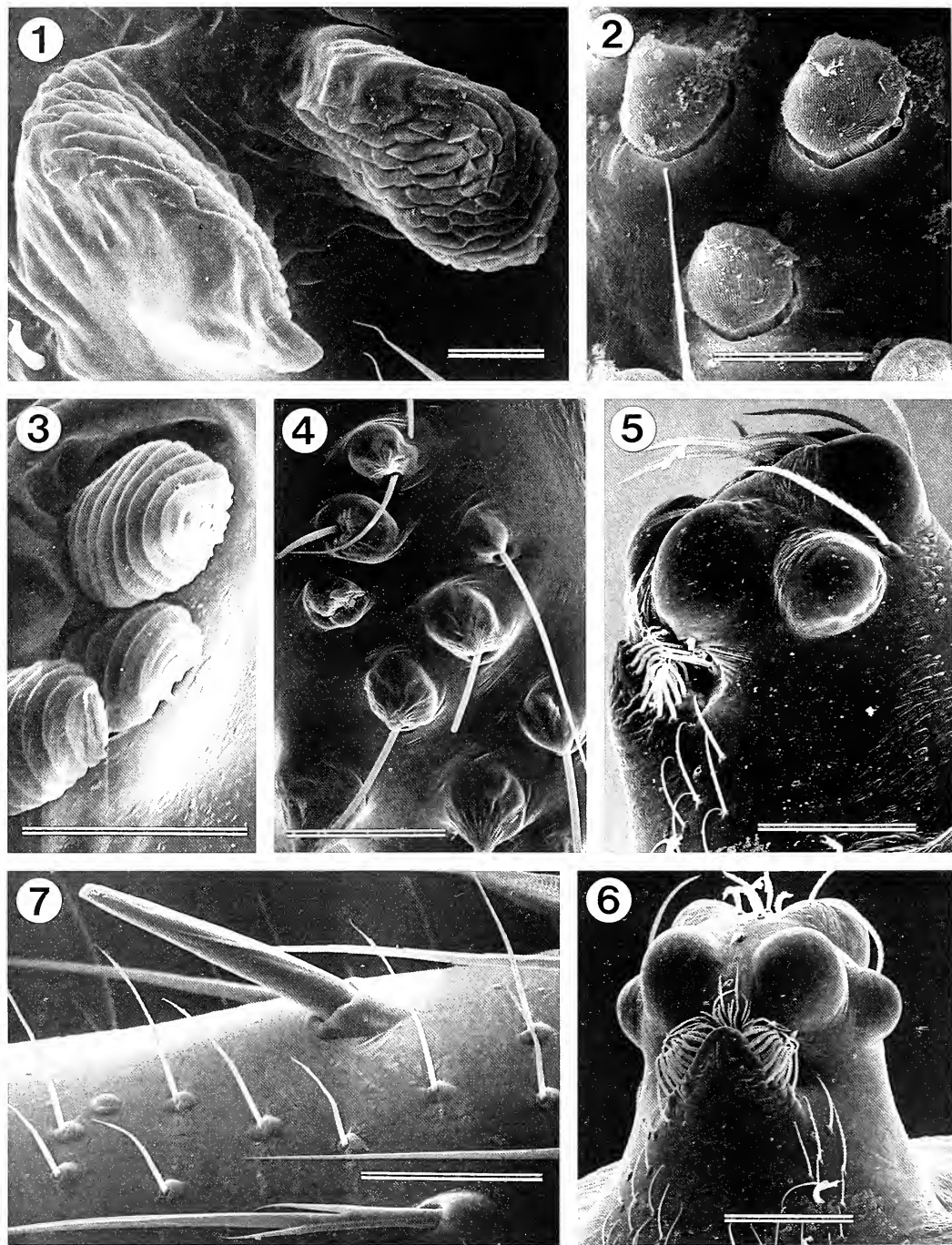
For reasons of space, I will focus on two

particular aspects: on non-genitalic contact structures which appear to evolve under selection similar to that acting on genitalia, and on the unusual phenomenon of copulatory courtship associated with vigor.

Voucher specimens of all unnamed species are deposited at the American Museum of Natural History, New York, and labeled with an I.D. number (“B.A.H. 1999 I.D.# 1–6”).

ARTFUL CHELICERAE

Pholcids are not unique in having species-specific copulatory contact structures (Eberhard 1985). However, pholcids are unique, at least among spiders, with respect to the wide range of non-intromittent male structures that are sexually modified (practically the entire palp is sexually dimorphic in most pholcids, including coxa and trochanter). Two male structures deserve special attention: the chelicerae and the clypeus. At least one of them contacts the female during copulation in all species studied (Huber 1994, 1995, 1997b, 1998b; Huber & Eberhard 1997; Uhl et al. 1995), and the chelicerae in particular are often the most species-specific and taxonomically useful structures. Modifications range from hairs of different shapes to cones, rounded, pointed, hooked and blade-shaped apophyses, and even to sexually dimorphic fangs (Figs. 1–4, 10, 11, 13, 14). Several hypotheses might explain this phenomenon: (1) reproductive isolation hypotheses (lock-and-key and genitalic recognition - reviewed in Eberhard 1985); (2) the “conflict of interest hypothesis” (Alexander et al. 1997); (3) sexual selec-



Figures 1–7.—Sexually dimorphic structures in male pholcids, SEM. 1. Cheliceral apophyses in *Uthina* sp. (I.D. #1); 2. Modified hairs on the chelicerae of *Modisimus dominical* Huber; 3. Modified hairs on the chelicerae of *Spermophora senoculata* (Dugès); 4. Sclerotized cones on the chelicerae of *Physocylus guanacaste* Huber; 5–6. Eye turret of *Modisimus culicinus* (Simon), in lateral and frontal view, showing frontal lobe; 7. Femur of *Modisimus tortuguero* Huber, showing a spine, a “normal” tactile sensillum, and several almost perpendicular hairs that cover the femora of only male walking legs. Scale bars: 0.01 mm (1–3); 0.05 mm (4, 7); 0.1 mm (5, 6).

tion by male-male competition (Eberhard & Briceño 1985); (4) the “sperm holder hypothesis” (Brignoli 1973); (5) sexual selection by female choice (Eberhard 1985, 1996).

Reproductive isolation hypotheses assume that species-specific differences in pholcid chelicerae evolved because they prevent hybridization. The lock-and-key version does this on a mechanical level, the genitalic recognition hypothesis on a sensory level. Both seem unlikely to account for the phenomenon in a general way. Often there is no female “lock”, for instance in most *Modisimus* species where the epigynum against which the male chelicerae are pressed during copulation is just a flat plate, but the chelicerae are nevertheless species-specific (Huber 1998a). Even in cases with a lock-and-key like fit, the hypothesis that such fit evolved to avoid cross-specific pairings is dubious because natural selection should favor early species recognition (Eberhard 1985, and references therein). However, transitory selection on cheliceral morphology in a species-isolation context cannot be ruled out, and may have been important in the past (Shapiro & Porter 1989).

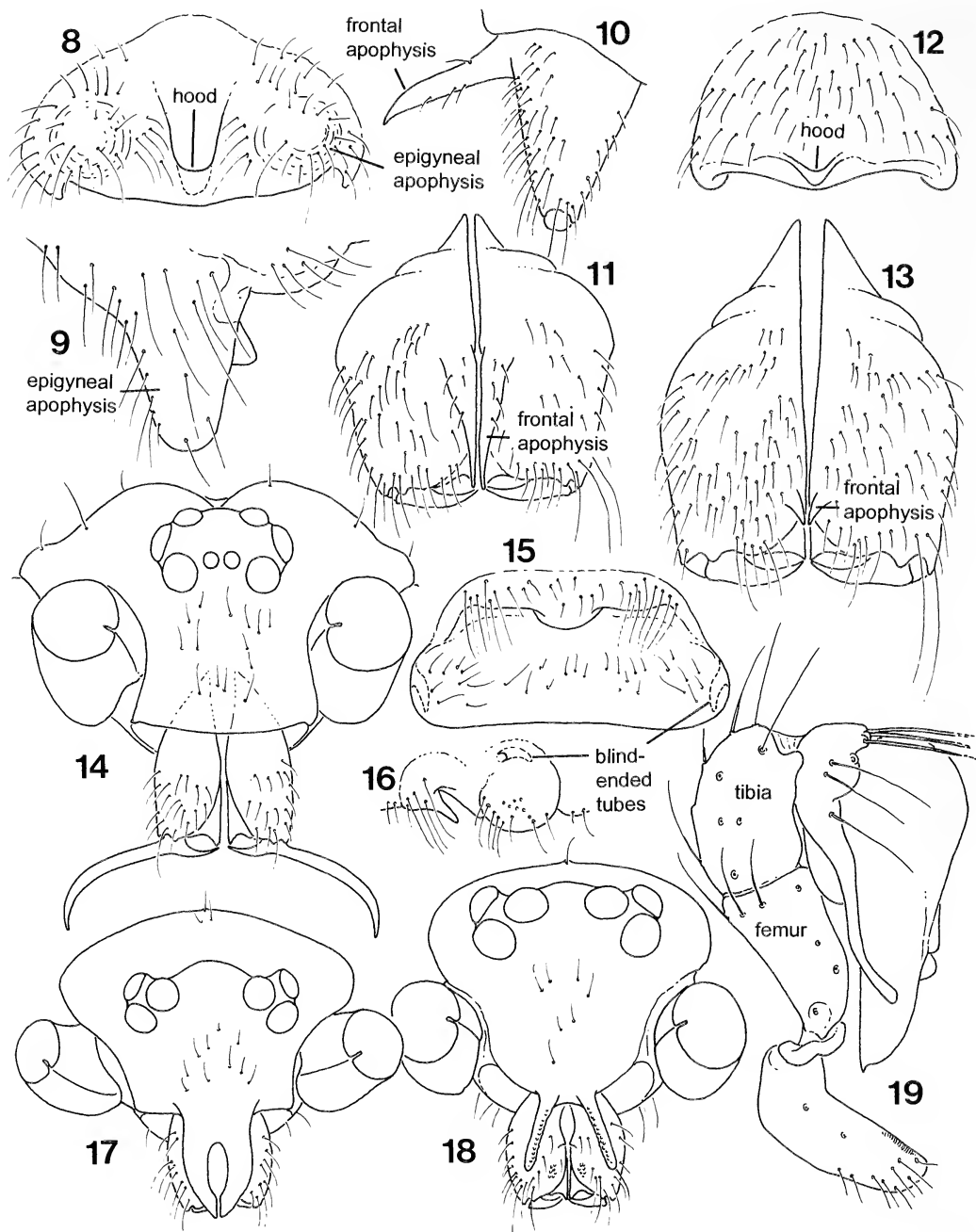
The “conflict of interest hypothesis” (Alexander et al. 1997), applied to pholcid chelicerae, would explain their often complex and species-specific design by physical coercive mating during which the male has to overcome female resistance and for this purpose uses his cheliceral modifications. One prediction is that one sex (usually the male) changes to increase the match and the other sex evolves to either decrease it or it does not evolve at all in that context (Alexander et al. 1997, p. 5). The data available for pholcids do not support this scenario. To the contrary, female epigyneal structures usually appear either neutral (flat plates) or even cooperative (hoods, grooves, pits, scapes) in that they help the male to lodge his chelicerae and thus to position his body correctly. It should be emphasized that conflict per se is of course not a distinguishing characteristic between the “conflict of interest” and the “female choice” hypotheses. Conflict is a necessary result of female choosiness, and some morphological details reflect this conflict particularly clearly: in a Peruvian pholcid (I.D. #2) the male presumably (judging by male and female morphology) lodges his cheliceral apophyses into a hood in the female epigynum. However, the

epigynum also carries a large apophysis on each side of the hood (Figs. 8, 9), so that only males with exceedingly long cheliceral apophyses can reach the hood (Figs. 10, 11). Thus, “genitalic arms races” of this sort may reflect selective female cooperation (the female provides a hood for those males able to overcome her obstructive apophyses) rather than female resistance to coercive males. Revealingly, the females of several putative close relatives have the cooperative structure (the hood) but not the barrier (the apophyses) (Fig. 12). Accordingly, their males’ cheliceral apophyses are rather inconspicuous (Fig. 13), but nevertheless species-specific in form.

Male-male competition is equally unlikely to provide a general explanation (Huber 1994). In most species the modifications seem highly inefficient for combat, and in some cases where their shape might suggest such a function (as in the Ecuadorian pholcid illustrated in Fig. 14; I.D. #3) the female morphology strongly indicates their use during copulation (the epigynum is unusually broad and at the lateral extremes provides two blind-ended cuticular tubes, whose location and spacing indicates that they are used to accommodate the male fang-apophyses: Figs. 15, 16). However, inter- and intrasexual functions are not mutually exclusive, and fighting with chelicerae must be considered a possibility in single cases.

Brignoli’s (1973) speculation that pholcid chelicerae may function to hold the sperm during sperm uptake is probably based on the observations of Gerhardt (1921–1933, references in Huber 1998d) that pholcid males make no sperm webs but transfer the drop of sperm to the chelicerae and take it up from there. This hypothesis obviously fails to explain why males should evolve such a variety of modifications to perform the same simple task of holding a drop of sperm.

Thus, by elimination, the hypothesis that seems to fit the available data best is cryptic female choice (as also for many other non-genitalic male contact structures - Eberhard 1985). Much like genitalia, chelicerae may function as copulatory courtship devices, whose elaborate morphology is used to stimulate or fit the female in a way that increases the male’s chances of fathering her offspring. In this hypothesis two main factors account for the diversity and relatively rapid evolution



Figures 8–19.—Characters discussed in the present paper. 8–9. Epigynum of a Peruvian pholcid (I.D. #2) in ventral and lateral (anterior side on left) view, showing the median hood and the lateral apophyses; 10–11. Male chelicerae of the same species, lateral and frontal view; 12–13. Epigynum, ventral view, and male chelicerae, frontal view, of '*Blechroscelis*' *cyaneotaeniata* (Keys.); 14. Portrait of an Ecuadorian species (I.D. #3), with modified fangs; 15–16. Epigynum of the same species, in ventral and lateral (anterior side on left) view, showing the blind-ended tubes into which the male apophyses are presumably inserted during copulation; 17–18. Clypeal modifications in two *Metagonia* species from Peru (17; I.D. #4) and Brazil (18; I.D. #5); 19. Right pedipalp of a Bolivian species (I.D. #6), in which the patella is reduced. Drawn to different scales.

of male chelicerae: the unpredictability of female criteria and the never ending competition among males for access to female eggs. How females evaluate the minimal differences among conspecific males' chelicerae, i.e., the sensory and neuroanatomical basis for doing so, remains an open question.

Sexual modifications of the male clypeus are less common in pholcids, but have apparently evolved several times convergently (e.g., in *Metagonia*: Figs. 17, 18, *Holocneminus* - Huber 1997b, Deeleman-Reinhold 1994). Like the chelicerae, the clypeal modifications are highly species-specific and in one species (*Metagonia rica* Gertsch 1986) it has been shown that they also contact the female genital area during copulation (Huber 1997b).

A special case of non-genitalic contact structure is the frontal lobe in male *Modisimus culicinus* (Simon 1893) (Figs. 5, 6). Clypeal glands open at the lobe, and during copulation the female mouth is in contact with the lobe, suggesting gustatorial courtship (Huber 1997a). However, the nature and function of the gland products are unknown (trigger female responses that are favorable to male? - signal the female that copulation has occurred? - nourish the female?) meaning that a decision between natural and sexual selection is not yet possible (see Eberhard 1996 for arguments linking sexual selection and male seminal products).

FORCEFUL GENITALIA

It has been noted that "details of copulatory courtship often seem to have little relationship to male size or vigor" (Eberhard 1997: 35). If this is the rule, then many pholcids might be exceptional: their genitalia are obviously their strongest organs (provided with the largest muscles), and in *Physocyclus globosus* (Tacz. 1873) this force is apparently used to rhythmically squeeze parts of the female genitalia during copulation (Huber & Eberhard 1997). Moreover, a morphometric study of genitalic and non-genitalic structures in the same species also apparently supported the notion that there is sexual selection on male vigor: fluctuating asymmetry (FA: deviations from perfect bilateral symmetry that are thought to reflect the degree of developmental stability) in large (strong) genitalia tended to be lower than in small genitalia (Huber 1996b). In the recent literature on FA such a negative re-

gression of FA on size is often interpreted as evidence for handicap models of sexual selection, in which only genetically "good" males can produce display structures that are both large and symmetric (Møller & Pomiankowski 1993; Watson & Thornhill 1994).

From a mechanical point of view, the pholcid male pedipalp works like a clamp, with the most distal segment (cymbium with procurus) acting against the femur. The economy of such a clamp is decreased by the two segments in-between (patella, tibia) and could be improved by elimination of one or both segments. In fact, in many pholcids (e.g., in *P. globosus*), the patella is functionally reduced in that part of the muscles of the femur insert in the tibia (Huber & Eberhard 1997) and not as usually in the patella (Ruhl & Rathmayer 1978). And in at least one species (sp. n. from Bolivia; I.D. #6) the reduction is complete, with the femur directly articulating with the tibia and no external trace of the patella left (Fig. 19). Yet another characteristic apparently functioning to increase the force applied to one critical point is realized in *P. globosus* (and probably in all *Physocyclus* species and in *Artema atlanta* Walckenaer 1837): the procuri are locked to each other, but the tip of only one is inserted into the female, moved by the muscular power of both pedipalps (Huber & Eberhard 1997).

Thus, there seems to be an ultimate advantage for males with strong palps, but the proximate function of this vigor is poorly understood. A possible solution may be in a structure of the female genitalia that is apparently unique to pholcids: the so-called "valve", an often complex "three dimensional zipper" between copulatory pouch (uterus externus) and oviduct (uterus internus). An apparent correlation has been documented between the strength and complexity of the "valve" and the strength of the male pedipalp (Huber 1998c). The correlation may be phylogenetically biased, however, so it is difficult to interpret.

It is not surprising that the recently intensified research on pholcids has raised more questions than it has answered. Thus, I would like to close this short review with yet another riddle. The males (but not females) of most species of several mainly Central American genera have the femora of their walking legs covered with short, almost perpendicular hairs

(Huber 1998a), resembling taste hairs (Foelix & Chu-Wang 1973) (Fig. 7). Nothing is known of these hairs, apart from the approximate systematic and geographical distribution of the character, the improbability of taste hairs being concentrated on femora, and the apparent lack of terminal pores necessary for chemosensory function.

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A COMPARISON OF THE RESPIRATORY SYSTEMS IN SOME CAVE AND SURFACE SPECIES OF SPIDERS (ARANEAE, DYSDERIDAE)

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ABSTRACT. We tested the hypothesis that the respiratory system of hypogean spiders is subject to regressive evolution by examining representatives of the family Dysderidae. This comparison included the epigean species *Dysdera ninnii* Canestrini 1868, and *Harpactea lepida* (C.L. Koch 1838), and the hypogean species *Stalita taenaria* Schiödte 1847, and *Parastalita stygia* (Joseph 1882). Both tube tracheae and book lungs of these species were measured and compared using 10 indices. Both the tracheal system and book lungs of the hypogean species were less developed than those of the epigean ones. We suggest that the cause is reduction of the respiratory system as a part of general structural reductions in the troglobites. This is consistent with the lower respiratory rates that characterize many troglobites.

True cave animals, called “troglobites,” are adapted to living in a very different environment from their surface relatives. Ecological conditions of the terrestrial underground environment are summarized here according to Vandel (1965) and Sket (1996). The most obvious and constant factor is the absence of light, consequently the absence of green plants and near absence of primary production, resulting in an energy-poor hypogean (subterranean) environment. The nearly constant temperature roughly equals the yearly average of the region. The chemical composition of the air in the caves that are well ventilated is similar to the surface atmosphere with a very slight increase of CO₂ concentration. However, in some caves CO₂ concentration may be significantly increased and O₂ concentration may be low (Vandel 1965; James *et al.* 1975; Whitten *et al.* 1987). Relative humidity in caves is normally 95–100%, so troglobites are hygrophilic and more sensitive to drying than epigean species (Vandel 1965).

Morphological adaptations of animals to the underground environment, or troglomorphisms, can be seen as gains or reductions. Typical hypogean arthropod gains are larger bodies and longer appendages, and increases in the number of “nonvisual” sensory organs.

Typically, cuticle features such as wings, pigmentation and eyes are reduced (Vandel 1965; Sket 1985). In European cave spiders, all possible stages of depigmentation, eye reduction, and weakening of the integument can be observed (Deeleman-Reinhold 1975) along with gains such as elongation of appendages.

Regressive evolution or degenerative evolution in cave organisms, reviewed by Fong & Culver (1985), Kane & Richardson (1985), Poulson (1985), Romero (1985) and Sket (1985) is not restricted to morphological regression but can also be met with physiological and ethological changes. Typical changes in hypogean animals include decreased metabolic rate, slower ontogenetic development, and pedomorphosis. The respiratory metabolic rates of the studied cave species were as low as 3% of that of related surface species in isopod crustaceans and as low as 14% in troglomorphic spiders (Vandel 1965; Hüppop 1985). The possible reasons of this reduction include relative ecological stability of the underground environment, lack of predators, low food availability (Hüppop 1985) and possibly higher CO₂ concentration (Whitten *et al.* 1987).

A number of authors present data about spider metabolism and respiratory physiology (e.g., Anderson 1970; Anderson & Prestwich 1980, 1982, 1985; Bromhall 1987; Dresco-Derouet 1969; Greenstone & Bennett 1980;

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Opell 1987, 1990, 1992, 1998; Paul *et al.* 1987, 1989; Paul & Fincke 1989; Paul 1992; Prestwich 1983a, 1983b; Strazny & Perry 1984, 1987). Energetic adaptations allow spiders to have roughly half the value of the metabolic rate present in other poikilothermic animals of the same weight. During starvation periods, which in spiders can be prolonged, they have the ability to lower metabolic rates below the resting values. Spiders that have the lowest metabolic rates are adapted to living in the energy-poorest environments. The measured metabolic rates show positive correlation to the respiratory surface and volume. Although the cited studies did not include any troglotic species, we can still assume that in the energy-poor cave environment the low metabolism in spiders can have impact on the structure of their respiratory system.

We studied the structure of the respiratory system in hypogean and epigean species of the spider family Dysderidae, which has many representatives in the Mediterranean, ranging from the most xerophilic epigean forms to the blind troglotites.

Dysderoidea includes families Dysderidae, Segestriidae, Oonopidae and Orsolobidae. Forster & Platnick (1985) claim that for Dysderoidea that their representatives have reduced book lungs, in the extreme case only four respiratory lamellae in some oonopids, and well developed paired tube tracheae, opening immediately behind the book lungs on the ventrolateral part of the abdomen. Levi (1967) and Winkler (1955) claim the above statement to be particularly adequate for Dysderidae.

In Dysderidae the tracheae extend into prosoma and enter the appendages (Winkler 1955; Novak 1967; Bromhall 1987; Foelix 1992). The dysderid heart is relatively small (Kaestner 1969). Spiders possessing prosomal tracheae have lower heart rates than spiders with tracheae limited to the abdomen (Bromhall 1987). The conclusion is that in Dysderidae the tracheae have a larger role in gas exchange than the book lungs, the latter being a less functional remnant of the evolution of this family.

We tested the hypothesis that reductions in the respiratory system occur during the course of evolution in phylogenetically old hypogean spider species. Thus, H_1 claims that the hypogean species have reduced respiratory sys-

tems relative to the epigean species. In contrast, H_0 states that there are no differences between hypogean and epigean species respiratory systems. The evidence supporting hypothesis H_1 is: (1) With few exceptions troglotites show lower metabolic rates than their epigean relatives; (2) High relative humidity in underground air coupled with thin integument of troglotic species might allow additional gas exchange through their body surface, so their respiratory system need not to be strongly developed; (3) The majority of European karst caves are well aerated (Gams 1974: p. 123), and the differences between the cave and the surface atmospheres in such cases are small (James *et al.* 1975). A significant increase of CO_2 concentration and corresponding O_2 concentration decrease in karst caves is a rather unusual phenomenon.

METHODS

Species studied.—For the study of the respiratory system four different dysderid species belonging to three subfamilies (Deeleman-Reinhold & Deeleman 1988) were chosen (number and sex of the studied specimens in parentheses): the epigean species *Dysdera ninnii* Canestrini 1868 of the Dysderinae (6♀) and *Harpactea lepida* (C.L. Koch 1838) of the Harpacteinae (5♂, 1♀), and the hypogean species of Rhodinae *Stalita taenaria* Schiödt 1847 (3♂, 3♀), and *Parastalita stygia* (Joseph 1882; 3♂, 2♀, 1 immature). All these species were collected in Slovenia. The exact locality and habitat data of the examined material is given elsewhere (Kuntner 1998).

Preparation.—Spiders were dissected in 70% ethanol in a petri dish. Dorsal surfaces of the prosoma and of the abdomen were carefully removed. The animals were then gently heated in 10% KOH for 1 hour. They were then placed in a vial filled with distilled water and the vial was rigorously shaken. All soft tissues, eroded by KOH were thus removed. The chitinous cuticle was then stained overnight in chlorazol black mixed with glycerol, all integumental structures (including both components of the respiratory system) being colored black. Later the preparation was examined in water or further dissected and measured in glycerol.

Parameters measured and indices calculated.—Abbreviations of measured parame-

Table 1.—Parameters measured. Units in millimeters or mm³ (*) except in NBL.

Abbre- via- tion	Parameter	Description
PL	Prosoma length	dorsal view
OL	Opisthosoma length	dorsal view
F4	Femur IV length	prolateral view
BSW	Book lung stigma width	ventrolateral view
TSW	Tracheal stigma width	ventrolateral view
TL1	Cranial tracheal trunk length	dorsal view of the outer length of the curved main tracheal trunk
TC	Cranial tracheal curvature width	dorsal view
TL	Actual cranial tracheal trunk length	calculated from TL1 and TC
TW	Cranial tracheal trunk width	width in the middle of the trunk
TV	Cranial tracheal trunk volume*	calculated from TL and TW
CTL	Caudal tracheal tube length	dorsal view
TP	Cranial tracheal profile	circumference of the terminal part of the cranial tracheal trunk was calculated from the measurement using drawing and curvimeter, taking into account only the profile from which the tracheolae originate
CTP	Caudal tracheal profile	circumference of the terminal part of the caudal tracheal trunk using the same method as above
NBL	Number of book lung lamellae	examined under light microscope laterally

ters, their names and short descriptions are given in Table 1. They were measured for each specimen, using dissecting and compound light microscope with a micrometer. For parameters TP and CTP we used scale drawings and curvimeter to calculate circumferences of tracheal parts. Parameters TL and TV were calculated using formulae from Bronštejn & Semendjajev (1984). Ten indices were devised (Table 2) to compare the size and development of the respiratory systems between species and to reduce the influence of body size on studied parameters. Features tend to vary with size, surface and volume of

the spider (*Harpactea lepida* was smaller in size than the rest of the species). This was taken into account in construction of indices as we tried to reduce variability of measured parameters within the pairs of surface and cave species.

Statistical analyses.—For analysis of differences among the surface and cave species, several statistical tests were applied: Wilcoxon rank sum (Mann-Whitney *U*-test), Kolmogorov-Smirnov, and Student *t*-test. Since different methods gave essentially the same results, only Wilcoxon rank sum is reported. There were generally no significant differences

Table 2.—Indices for comparison of the respiratory systems in species examined. Parameter abbreviations given in Table 1. Structure-index composition: L = length, S = surface, V = volume, N = number.

Quotient	Description	Structure
I1	TL/PL ³	Relative cranial tracheal trunk length L/V
I2	TW/PL	Relative cranial tracheal trunk width L/L
I3	TV/PL ⁵	Relative cranial tracheal trunk volume V/(S.V)
I4	CTL/PL ³	Relative caudal tracheal tube length L/V
I5	TP/PL ²	Relative extent of tracheolae branching in the prosoma L/S
I6	CTP/OL ²	Relative extent of tracheolae branching in the opisthosoma L/S
I7	TP/F4 ²	Relative extent of tracheolae branching in the appendages L/S
I8	TSW/PL ²	Relative tracheal stigma width L/S
I9	BSW/PL ²	Relative book lung stigma width L/S
I10	NBL/PL	Relative number of book lung lamellae N/L

Table 3.—Wilcoxon rank sum test of differences between species and species groups: — Not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Index	Comparison		
	<i>Stalita:</i> <i>Parastalita</i>	<i>Dysdera:</i> <i>Harpactea</i>	Cave: Surface
TL/PL ³	—	—	—
TW/PL	—	—	**
TV/PL ⁵	—	—	**
CTL/PL ³	*	—	***
TP/PL ²	—	—	***
CTP/OL ²	—	—	—
TP/F4 ²	**	—	***
TSW/PL ²	—	—	***
BSW/PL ²	—	—	*
NBL/PL	—	—	***

among the cave or surface species (Table 3), so combined samples were eventually used to test the differences between cave and surface groups of species.

RESULTS

Both hypogean species lack eyes and have longer legs than both epigean species. In addition they are depigmented, have more setae on their legs, and appreciably more delicate cuticle. *Dysdera ninnii* has a well-developed tracheal system, but both cave species have less extensive tracheae. Although *Harpactea lepida* has relatively stout cranial tracheal trunks, these are relatively shorter than those of *D. ninnii*. However, no significant difference in all the indices between both surface species was observed (Table 3). Similarly, there was no significant difference in most of the indices between both cave species, the indices I4 and I7 being an exception (Table 3). Figure 1 shows the values of indices I1 to I10 for the studied species in the same order as listed in Table 2 (in the graphs the names of genera are given). In Table 3, Wilcoxon rank sum test of differences between both species pairs are presented.

Relative cranial tracheal trunk length (I1) was largest in *D. ninnii*, followed by *H. lepida* and both cave species. However, there was no significant difference between the epigean and hypogean pairs of species. Relative cranial tracheal trunk width (I2) showed similar values in both epigean species and was lower in

both troglobites, both pairs of species showing significant difference. Relative cranial tracheal trunk volume (I3) showed a similar result to the previous index. Relative caudal tracheal tube length (I4) showed highly significant difference between both species pairs, and so did the next index—relative extent of tracheolae branching in the prosoma (I5). Relative extent of tracheolae branching in the opisthosoma (I6) was lower in the epigean pair of species, both species pairs showing no significant difference. Relative extent of tracheolae branching in the appendages (I7) was highest in *D. ninnii*, followed by *H. lepida*, *S. taenaria* and was lowest in the longlegged (more troglomorphic) *P. stygia*. There was a highly significant difference between the pairs of species. Relative tracheal stigma width (I8) was similar within the cave and surface species groups and showed a significant difference between them. The values for the relative book lung stigma width (I9) were again significantly higher in the epigean pair of species. Relative number of book lung lamellae (I10) showed again significantly higher values for the surface versus cave species pairs.

DISCUSSION

Dysdera ninnii has the most extensive tracheal system of the examined species. Both cranial and caudal tracheal trunks are strongly developed, and they branch into numerous tracheolae that supply with oxygen the prosomal organs, appendages and opisthosoma. Book lungs are also well developed, having up to 23 lamellae, but show considerable variability in their size (Kuntner 1998). The second epigean species, *Harpactea lepida*, shows similarly developed tracheal system and book lungs to *D. ninnii*, despite its smaller size. Although *H. lepida* and *D. ninnii* are both forest species, different ecological factors might influence their anatomy and physiology. However, as hypothesized, the examined surface species exhibit a well-developed respiratory system, even though they belong to different subfamilies.

The troglobites, *Stalita taenaria* and *Parastalita stygia*, both show reductions in the tracheal as well as book lung systems, compared to both surface species. Their cranial tracheal trunks are relatively shorter, narrower, and not as curved as in *D. ninnii*. They extend further into prosoma through the petiole be-

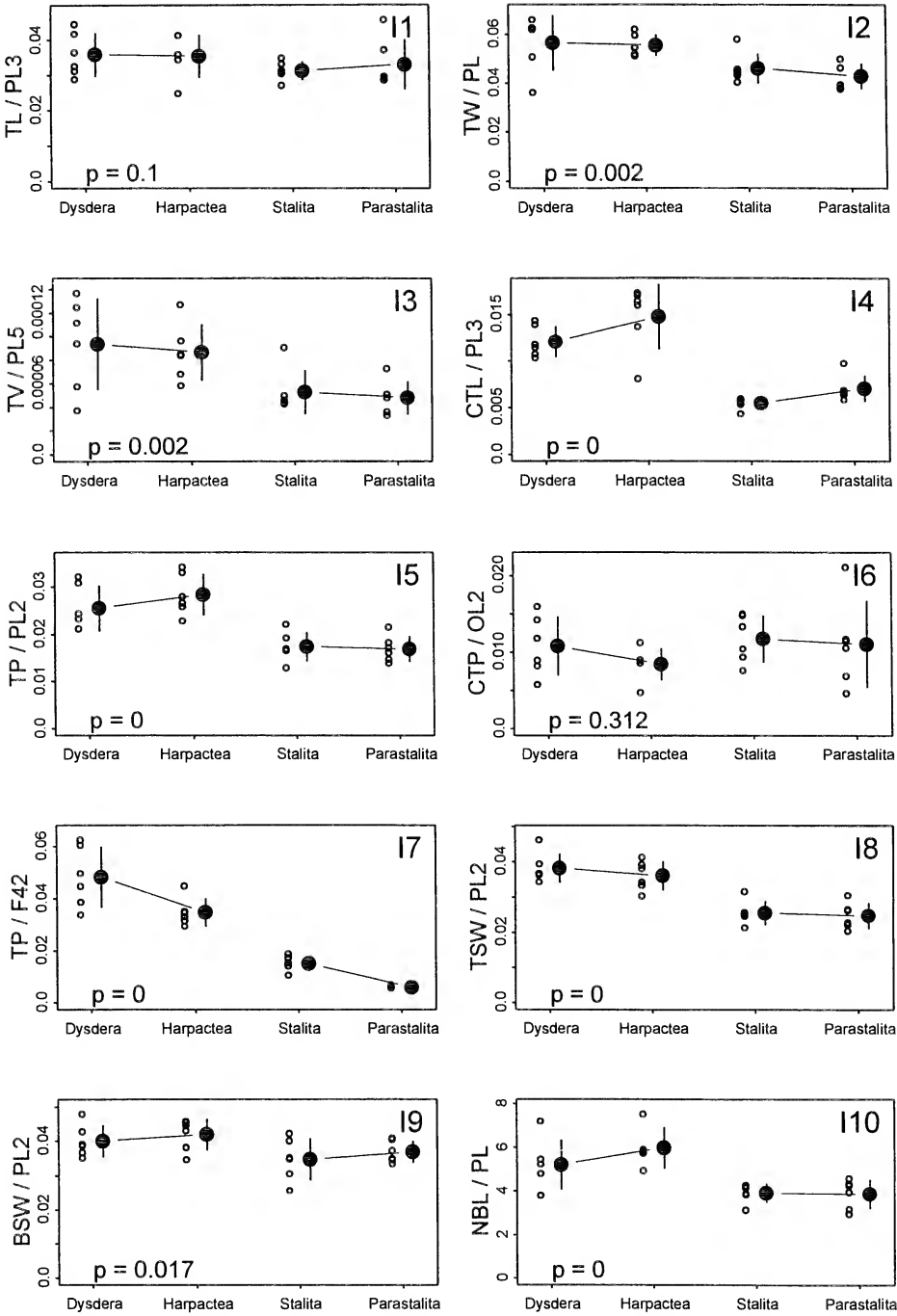


Figure 1.—Relative size and development of the respiratory system in epigeal (*Dysdera ninnii*, *Harpactea lepida*) and hypogean (*Stalita taenaria*, *Parastalita stygia*) dysderid spiders from Slovenia, measured in six specimens each. For explanation of indices (I1–I10) see Table 2. (○ = Individual data, ● = Mean value ± SD, p = Wilcoxon rank sum significance level for differences between the surface and cave groups of species, groups indicated by the lines connecting mean values).

fore branching into tracheolae. The tracheolae bundle is much weaker in prosoma and fewer were observed to enter the legs. Their caudal tracheal tubes are greatly reduced compared to the ones in surface species, but the extent of the tracheolae branching in the opisthosoma shows no difference. The book lungs of both troglobites are also reduced and have a slightly different general appearance from those in the epigeal species.

Both hypogean species showed very similar values of all the indices. Since they belong to a different subfamily than *Dysdera* and *Harpactea*, we cannot be sure that the supposedly epigeal ancestors of hypogean Rhodinae had a stronger developed respiratory system, similar to that of *Dysdera* and *Harpactea*. However, we speculate that in both cave species it has been subject to regressive evolution. There are no comparable data on cave spider respiratory morphology in available araneological literature (e.g., Nentwig 1987). Yet, this seems to be another example of structural reduction in troglobites, similar to the reduction of other originally integumental structures in troglobitic spiders (Deeleman-Reinhold 1975) and other arthropods (Vandel 1965; Sket 1985). The cause for the reduction of the respiratory system in cave spiders still needs to be investigated further.

Opell (1990, 1998) states that tracheae and book lungs in the spider family Uloboridae are complementary respiratory structures; when one system is better developed the other is reduced. Opell concludes that the development of the two systems is governed by both spider's total respiratory demands and by the specificity of these demands. The more active species (with reduced webs) have relatively better developed tracheae, and the less active (orb-weaving) species have relatively better developed book lungs. If this is true for Dysderidae, future research could focus on possible compensating changes in both systems. Are both systems reduced in the troglobites or is there a shift in relative development of each system? As our study primarily treated the dysderid tracheae, future studies may reveal that the book lungs in the hypogean environment are more useful than in the epigeal one.

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A NEW ALL-FEMALE SCORPION AND THE FIRST PROBABLE CASE OF ARRHENOTOKY IN SCORPIONS

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ABSTRACT. A new parthenogenetic species of scorpion, *Ananteris coineau* Lourenço, is reported from French Guyana. Parthenogenesis is based on the production of an all-female brood (thelytoky) by a wild virgin female. Conversely, the first probable case of male parthenogenesis (arrhenotoky) in scorpions is reported based on the production of two successive all-male broods by a wild caught virgin female of *Tityus metuendus* Pocock from Peru. Both species were found in isolated palm trees within the rain forest, conforming with the insular theory of parthenogenesis.

With the exception of mites, all-female reproduction is quite rare within the order Arachnida (Taberly 1987; Palmer & Norton 1991; Norton & Palmer 1991; Nagelkerke & Sabelis 1991), but has also been demonstrated in a few species of harvestmen (Tsurusaki 1986), spiders (Lake 1986; Deelman-Reinhold 1986; Camacho 1994) and scorpions (Lourenço & Cuellar 1994). Among the almost 1500 species of scorpions throughout the world, only five are known to be parthenogenetic (Lourenço & Cuellar 1994). The first case was reported by Matthiesen (1962) in the Brazilian species *Tityus serrulatus* Lutz & Mello. Wild pregnant females were collected and their all-female progeny reared individually, giving virgin birth to a second all-female generation several months later. Matthiesen's findings were later confirmed by San Martín & Gambardella (1966). Since then, *T. serrulatus* has been relegated to *Tityus stigmurus* (Thorell) (Lourenço & Cloudsley-Thompson 1996) a parthenogenetic species consisting of at least four distinct all-female morphs (Lourenço & Cloudsley-Thompson this volume) of which the original *T. serrulatus* is one. The other four parthenogenetic species are *Tityus uruguayensis* Borelli from Uruguay and Brazil, *Tityus columbianus* (Thorell) from Colombia, *Hottentota hottentota* (Fabricius) from West Africa, and *Liochelis australasiae* (Fabricius) from the South Pacific (Lourenço & Cuellar 1994). *Tityus trivittatus* Kraepelin

from Argentina is also suspected of parthenogenesis (Peretti 1994; Maury 1997). In this paper, we report an additional parthenogenetic scorpion (*Ananteris coineau* Lourenço from French Guyana), and the first observation of all-male broods in scorpions (*Tityus metuendus* Pocock from Peru).

METHODS

Scorpions were raised individually in plastic boxes terraria, with different sizes ranging from 6/5/4 to 36/14/24 cm. The bottom of each terrarium was covered with a soil layer and water was supplied in Petri dishes. Food, consisting on crickets and spiders of the genus *Pardosa*, was supplied once a week. The terraria were placed in a room where temperature was maintained at $25^{\circ}\text{C} \pm 2^{\circ}\text{C}$. Humidity ranged from 60–70%.

The sex of individuals was determined by the examination of the size and sexual dimorphism of the pectines. For details and illustrations see Farzanpay & Vachon (1979) and Lourenço (1983).

When life cycles are completed, voucher material will be deposited in the Natural History Museum, Paris (*A. coineau*) and in the Zoologisches Museum of the University of Hamburg (*T. metuendus*).

RESULTS

***Ananteris coineau* Lourenço.**—*Ananteris coineau* was described from a rain forest near

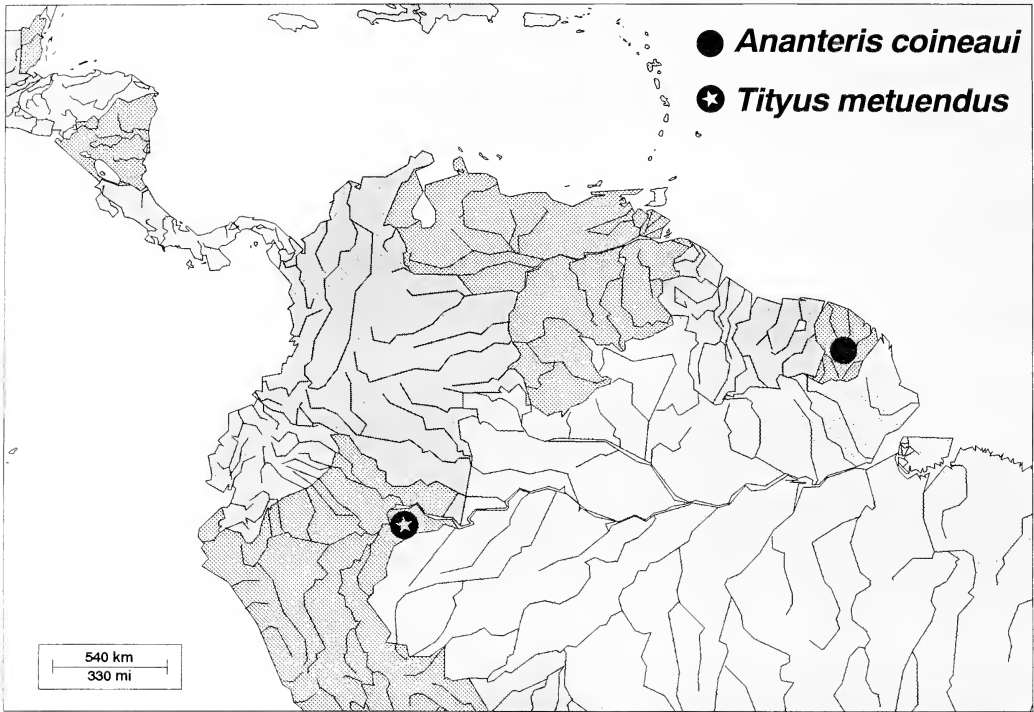


Figure 1.—Map showing the areas where the parthenogenetic females of *Ananteris coineau* and *Tityus metuendus* have been collected.

the Arataye river in French Guyana, based on three adult females collected in a palm tree of the species *Astrocaryum paramaca* Martius (Lourenço 1982; Kahn 1997). Since then, only

one additional specimen was collected from Saül (close to the original locality), also in a palm tree. Within about two weeks, the female molted; by March 30, she gave birth to 16

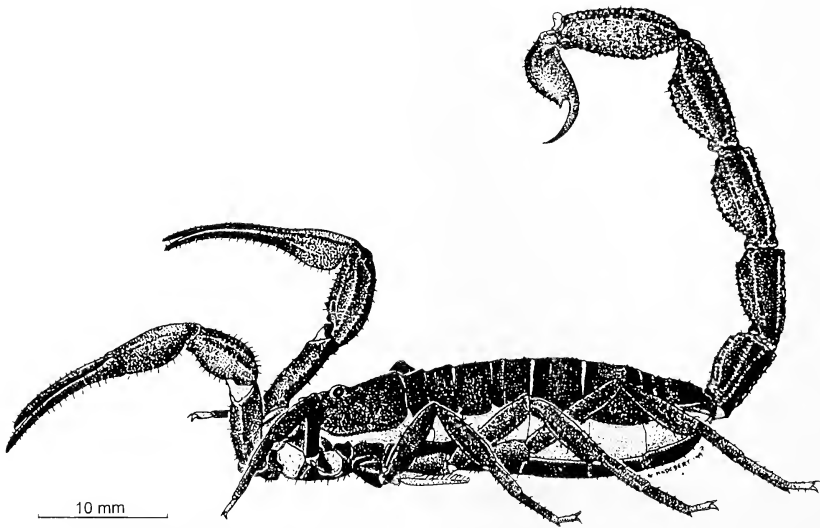


Figure 2.—The parthenogenetic female of *Tityus metuendus*.

young, which remained on her back until April 6 when they all died before molting. An examination of the size and sexual dimorphism of the pectines revealed that the entire brood consisted of females, suggesting parthenogenesis. *Ananteris coineai* is probably endemic to the central region of French Guyana, and based on the rarity of field specimens, probably has a very low population density. Since this genus was created by Thorell in 1891, the number of species described is now 20 (Loureño 1997a). The number of specimens representing these species remains very small (less than 200), suggesting that most species are rare. Only the original species described by Thorell, *A. balzani*, seems abundant and has a much larger range of distribution (Loureño 1993). Nearly 50 specimens of *A. balzani* were collected since 1975, with a sex ratio of approximately 1♂:2♀. Of the remaining 19 species, 12 are represented by less than 5 specimens each, and 4 by only a single specimen. Males are rare, having been found in only 10 of the 19 species.

As noted by Camacho (1994) for spiders, female-biased sex ratios may be taken as evidence of parthenogenesis. This could also be true for the genus *Ananteris* and other microscorpions in which males are rare or absent. With the exception of a recent study on reproductive effort between sexual and parthenogenetic populations of *Tityus columbianus* (Loureño et al. 1996), virtually nothing is published on the life history and behavior of parthenogenetic scorpions.

The occupancy of isolated palm trees within vast areas of rain forest or savanna conforms with the concept of insular parthenogenesis proposed by Cuellar (1977, 1994). Most well studied parthenogenetic animals occur in insular habitats such as isolated caves, spring heads, bogs, termite nests, rotting logs, tree trunks, hibernacula and oceanic islands (Cuellar 1994). Most parthenogens are also characterized by small size, low mobility, and low population density (Cuellar 1994). The rarity of *A. coineai*, its occurrence on isolated palm trees, and the absence of males all suggest a parthenogenetic mode of reproduction. This may hold as a rule for other species in this genus.

***Tityus metuendus* Pocock.**—*Tityus metuendus* is a rain-forest species distributed mainly in western Amazonia between Brazil

and Peru. In the vicinity of Manaus, Brazil, specifically the Ducke Reserve, the populations of *T. metuendus* are strictly sexual with a sex ratio of 1/1 (Loureño 1983, 1997b). During some recent collections (1996) in the Amazonian region of Peru, near Iquitos (town of Jenaro Herrera), a single pre-adult female of *Tityus metuendus* was collected by Dr. G. Couturier (Orstom-Muséum) from a palm tree of the species *Astrocaryum chambira* (Kahn 1997) and brought to one of us (WRL). On 18 October 1996, about seven months after the last molt, this female gave birth to a brood of 21 neonates, of which only three survived to the adult stage, all males. An examination of the pectines of the remaining preserved immatures revealed that the entire brood was male. On 29 September 1997, the same female produced a second brood of 32 neonates, of which three did not complete embryological development and 29 were normal. The normal ones all died a few days later after the first molt. As with the previous brood, examination of the pectines revealed only males. A third all-male brood was observed on the 30 April 1998.

The production of three consecutive all-male broods by this virgin female may well represent the first case of arrhenotoky in scorpions, and possibly among Arachnida other than Acari (Nagelkerke & Sabelis 1991). No data are presently available in scorpions either to explain the meiotic mechanisms of arrhenotoky or its evolutionary significance (Bull 1983), as exist for other groups such as the Hymenoptera (Waage 1986; Cuellar 1987) and mites. According to Taylor & Sauer (1980), a major selective advantage of arrhenotoky compared to diploidy is that mothers can precisely determine sex ratio by controlling the fertilization of each egg. This is particularly advantageous in species with finite mating groups, in which the probability is high that some clutches may contain no males (Nagelkerke & Sabelis 1991), or that the sex ratio may be biased in favor of females (Charnov 1982). Precise sex ratios have been documented in several arrhenotokous species of parasitic wasps (Waage 1986), which lay their eggs either in a single host or a clumped group of hosts. In phytoseiid mites, pseudo-arrhenotoky has apparently arisen as a consequence of low mobility and a subdivided population structure. Their dominant prey form patchy in-

festations which are probably invaded by only a few females, leading to very small mating groups (Nagelkerke & Sabelis 1991). Similar mating conditions may exist for *T. metuendus*, but extensive field work is needed to understand its life history and behavior.

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DISCOVERY OF A SEXUAL POPULATION OF *TITYUS SERRULATUS*, ONE OF THE MORPHS WITHIN THE COMPLEX *TITYUS STIGMURUS* (SCORPIONES, BUTHIDAE)

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ABSTRACT. *Tityus serrulatus* Lutz & Mello 1922 (in fact, the form confluenciata within the *Tityus stigmurus* complex) is an extremely toxic scorpion of considerable medical importance in Brazil. Its rapid spread is partially due to parthenogenesis. Speculation regarding the occurrence of sexual individuals has been resolved by the discovery of a population, described here, having a male-female sex ratio of 1/2.5. Four color morphs of the *T. stigmurus* complex are described, and it is concluded that *T. serrulatus* and *Tityus lamottei* Lourenço 1981 are junior synonyms of *T. stigmurus* (Thorell 1877).

Scorpionism is well known in Brazil and has been documented there since the end of the 19th century. Two species are currently associated with most incidents of medical importance, *Tityus serrulatus* Lutz & Mello 1922 and *Tityus bahiensis* (Perty 1934). The first comprehensive study of the phenomenon of scorpionism was that of Maurano (1915); this work, however, dealt primarily with *Tityus bahiensis* (Perty), the second most toxic species in South America. This species was originally described from Brazil. In recent years, the geographic range of the Brazilian scorpion *T. serrulatus* has increased considerably (Lourenço & Cloudsley-Thompson 1996). In Brazil, this species poses an exceptional health problem due to its rapid expansion in urban areas, its sudden proliferation and its great toxicity.

Since the description of *Tityus serrulatus*, most attention has been focused on its medical importance. However, it was observed that males are absent from all known populations, and Matthiesen (1962) first demonstrated that this species reproduces by parthenogenesis. This phenomenon although rare, has been demonstrated in other species of scorpions, also (Lourenço & Cuellar 1994). *Tityus serrulatus* was considered to be an obligate parthenogenetic species because bisexual populations had not been detected. Moreover, the apparent absence of related bisexual individ-

uals within its known geographic distribution suggested that the generating species either had been eliminated after giving rise to parthenogenesis, or that *T. serrulatus* evolved elsewhere and has since occupied an extensive region from which its bisexual progenitors were absent (Lourenço & Cuellar 1994; Lourenço & Cloudsley-Thompson 1996; Lourenço et al. 1996).

METHODS

The specimens of the sexual population of *Tityus serrulatus* were collected during daytime and were found under logs and bark. The area where this population was located presents a transitional vegetation type ranging from dry forests and cerrados to caatingas. In contrast, parthenogenetic populations are only known from modified sites and are often found inside cities and towns, where they live inside houses, but are also frequent in cemeteries and even in the sewer system. For details see (Lourenço & Cuellar 1995; Lourenço & Cloudsley-Thompson 1996; Lourenço et al. 1996).

Identification of sex was based both on external features and on dissection of adult males and females. The voucher material concerning the sexual population of *Tityus serrulatus* is partially deposited in the Natural History Museum in Paris, but also in the Ezequiel Dias Foundation in Belo Horizonte, Brazil.

RESULTS AND DISCUSSION

Lourenço (1981) suggested that *T. serrulatus* was closely related to *Tityus stigmurus* (Thorell 1877), a bisexual species with a range of distribution further north of *T. serrulatus*. Several other authors had discussed the status of these two species and their possible relationship. In the opinion of some (Pessoa 1935; Mello-Leitão 1939; Eickstedt 1983), both species should be considered distinct. Others asserted that, before about 1920, *Tityus stigmurus* had been a common species in the central and southern regions of Brazil (States of Minas Gerais, São Paulo and Goiás), and that the two species are varieties of a single species (Mello-Campos 1924; Vellard 1932). A few years ago, Lourenço (unpubl.) checked the notes of Vellard and some of his collected material. This confirmed that *Tityus stigmurus* was undoubtedly a common species in the State of Minas Gerais and south of Goiás, until at least the 19th Century (Lourenço & Cloudsley-Thompson 1996).

Lourenço & Cloudsley-Thompson (1996) and Lourenço et al. (1996) suggested that the sexual and the parthenogenetic populations of a complex *T. stigmurus*/*T. serrulatus* might correspond respectively to the northern range of *T. stigmurus* and the southern range of *T. serrulatus* in Brazil. However, recent unpublished field observations by Lourenço show that both the morphs *T. serrulatus* (= *confluenciata*) and *T. stigmurus* (= *unifasciata*) reproduce by parthenogenesis. Moreover, the sexual individuals of *T. stigmurus* occur in an undisturbed region of Exu in the State of Pernambuco, whereas the parthenogenetic populations are found among human communities along the coastal regions of its northern range.

Two other sexual morphs (*confluenciata*/*maculata* and *trifasciata*) occur in undisturbed regions. The first corresponds to the species described by Lourenço (1981) as *Tityus lamottei*. It occurs in a transitional zone between two major natural ecosystems, Cerrados and Caatingas in the western part of the State of Bahia, whereas *trifasciata* occurs in the State of Ceará at the extreme northern end of its range. Although these species are at present sexual, we speculate that future human disturbance could possibly lead to their replacement by parthenogenetic counterparts (see Louren-

ço & Cuellar 1995; Lourenço & Cloudsley-Thompson 1996) (Fig. 1).

Recent field observations on the polymorphic patterns of pigmentation (Lourenço in press) suggested that the above distinction between *T. stigmurus* (= sexual) and *T. serrulatus* (= parthenogenetic) forms, is not sufficiently comprehensive. The following classification of color morphs is therefore proposed: (a) Morph *unifasciata*: with a single median longitudinal dark stripe over the body as observed in the species named *T. stigmurus* (Thorell 1877). (b) Morph *confluenciata*: with confluent dark spots over the tergites as observed in the species named *T. serrulatus* Lutz & Mello 1922. (c) Morph *confluenciata/maculata*: with the same pattern as in b, but with dark spots over the pedipalps and legs, as observed in the species named *T. lamottei* Lourenço 1981. (d) Morph *trifasciata*: with three longitudinal dark stripes over the body as observed on an undescribed population from the State of Ceará. Other patterns probably exist but have not yet been documented.

Where the sexual populations of the *confluenciata* (= *T. serrulatus*) form are distributed remains unsolved. Recently a sexual population was located by one of the authors (WRL) in the north of the State of Minas Gerais, Brazil, in the region of Irapé close to the Jequitinhonha river (Fig. 1).

A sample of 39 specimens containing 12 males, 27 females and immature individuals of different instars was collected, giving a sex-ratio of 1 to 2.25 in favor of females. This is close to the sex-ratios observed in other species of *Tityus* (Lourenço, 1980). Detailed examination of all these specimens revealed few differences from the morphology of the parthenogenetic population. The pattern of coloration is very similar in both males and females, and in both sexual and parthenogenetic populations. The general morphology of the females is also similar in both the sexual and the parthenogenetic populations, with the exception of body size which seems to be slightly larger and bulkier in the sexual females. The general morphology of the males is quite different, however, from that of the females. The pedipalps are longer and more slender (Figs. 2, 3). The pectines are larger although the total number of teeth is almost the same in both sexes: males, 22–27; females, 22–26.

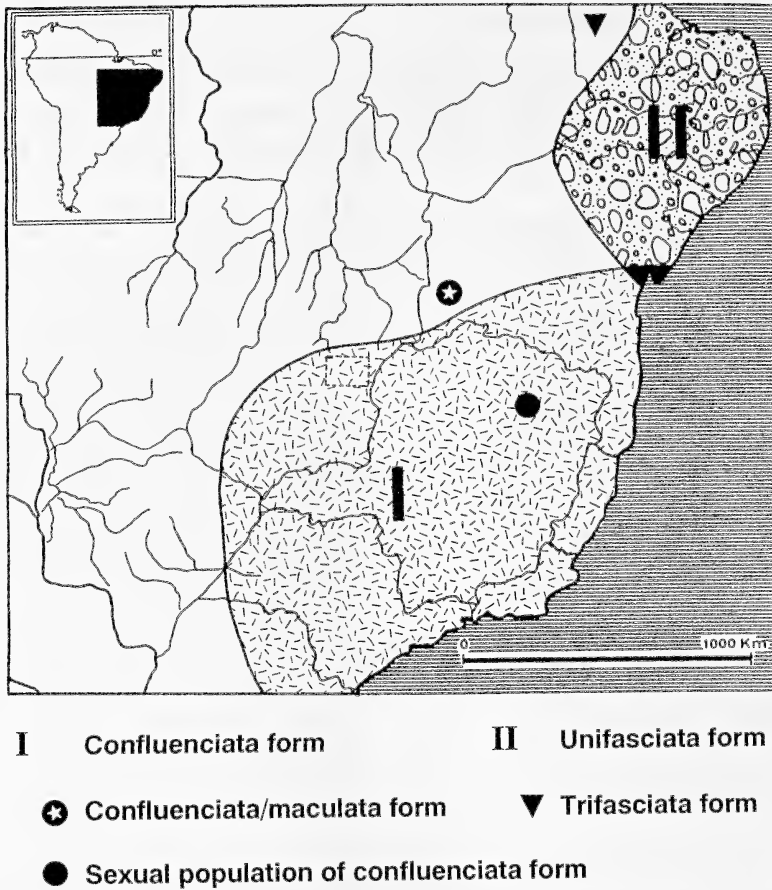


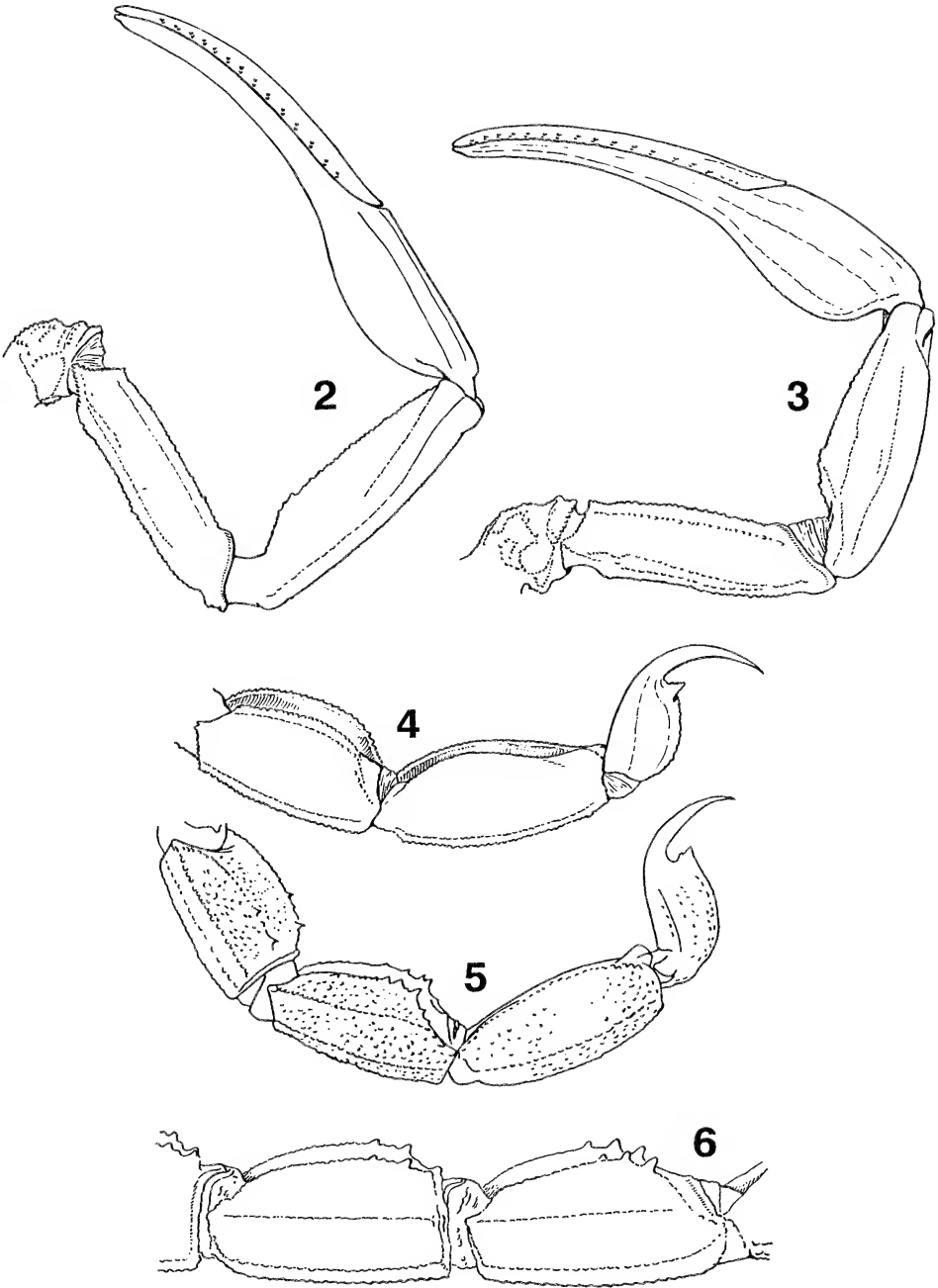
Figure 1.—Present geographical distribution of *Tityus stigmurus* (morph *unifasciata*) and *Tityus serrulatus* (morph *confluenciata*). The black represents the contact zone between the two populations. In detail, the localities where *Tityus lamottei* (morph *confluenciata/maculata*), morph *trifasciata* and the sexual population of *T. serrulatus* have been collected.

The first two differences characterize males of many species (Polis & Sissom 1990).

One major morphological difference was, however, observed between the sexual and parthenogenetic populations. The typical trait which characterizes the parthenogenetic population, as suggested by the Latin name "*serrulatus*", is the presence of granules modified as spines on the posterior region of the dorsal keels of metasomal segments III and IV. The number of spines varies from 2–10. In the sexual population, these spines were present in the immature instars, but disappeared after the last molt and were absent in adults (Figs. 4–6). This difference cannot yet be explained but is almost certainly associated with genetic differences between the two populations corre-

lated with their modes of reproduction. Further studies on the biology of the sexual population are required.

Diagnosis of the sexual *confluenciata* form.—Scorpions of medium size ranging from 55–70 mm in total length. General coloration yellowish. Metasoma: segments I to V yellowish with blackish lateral and ventral spots: 10-10-8-8-5 keels present. The dorsal keels of segments III and IV with the posterior granules modified as spines varying in number from 8–10, only present in immature instars; absent from adults. Dentate margins of pedipalp-chela fingers composed of 13–17 oblique rows of granules. Telson with a long curved aculeus; subaculear tooth strong and spinoid. Pectines with 22–27 teeth; slightly



Figures 2-6.—Morphological characters of sexual and parthenogenetic populations of the *confluenciata* form. 2, 3. Pedipalps in dorsal view of male and female sexual individuals showing dimorphism; 4. Metasomal segments IV, V and telson in lateral view of an adult sexual female showing the absence of typical spines; 5. Metasomal segments III to V and telson, in lateral view, of an adult parthenogenetic female population showing the typical spines; 6. Same with metasomal segments III and IV in detail.

greater than that observed in the parthenogenetic population (19–24) (see Lourenço & Eickstedt 1981).

For nomenclatural correctness, only the name *Tityus stigmurus* (Thorell 1877) should be retained, while *Tityus serrulatus* Lutz & Mello 1922 and *Tityus lamottei* Lourenço 1981 must be considered as junior synonyms of *Tityus stigmurus*. The designations *unifasciata*, *confluenciata*, *confluenciata/maculata* and *trifasciata* provide a practical way of identifying the different forms.

Phylogenetic work at the molecular level would be of great value for a better definition of the genetic relationships among the different forms of the *Tityus stigmurus* complex. A beginning has already been made and this molecular work is in progress with research teams in Mexico and Brazil.

ACKNOWLEDGMENTS

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ACTIVITY RHYTHMS AND BEHAVIORAL CHARACTERIZATION OF TWO EPIGEAN AND ONE CAVERNICOLOUS HARVESTMEN (ARACHNIDA, OPILIONES, GONYLEPTIDAE)

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ABSTRACT. The activity rhythms, feeding behavior, and reaction to light of two epigeal (surface inhabitant) species of harvestmen (*Iporangaia pustulosa* and *Iguapeia melanocephala*) and of one cavernicolous species (*Pachylospeleus strinatii*) have been recorded. Both the epigeal and the cavernicolous species showed a highly pronounced circadian rhythmicity. The cave species showed a bimodal pattern. Whereas the epigeal species carried food away to feed, the cave species fed where they found the food. The time of reaction to light did not differ statistically between species. However, when exposed to light, the cave species walked much longer distances after it started walking. These differences are probably due to cave adaptation. The cave species may have to wander further for food (and maybe mates) because of the scarcity of resources and, therefore, show greater activity and also a tendency to exploit a resource wherever they find it.

The cave environment is characterized by darkness, at least in deep regions, and the consequent reduction or absence of photoautotrophic organisms, high relative humidity (almost 100%), and small temperature variations over both a daily and annual basis (Barr 1968; Poulson & White 1969; Howarth 1983). These peculiar conditions promote the establishment of a characteristic fauna which may possess morphological, physiological and behavioral modifications that allow them to find food and sexual partners (Culver 1982; Parzefall 1986; Holsinger & Culver 1988), especially among species restricted to the subterranean environment (the troglobites). These modifications may include reduction or loss of eyes and pigmentation, improvement of other sensorial organs, etc. Behavioral patterns that have lost their biological meaning in the new habitat (e.g., avoidance of predators, which may be absent) or for which a cue is absent (e.g., those behaviors related to vision) could be suppressed in the troglobites. In turn, new behavioral patterns related to the new habitat conditions may arise.

One of the most conspicuous biological differences between troglobitic and epigeal species is related to endogenous, self-sustained biological rhythms. Because surface environ-

mental conditions oscillate cyclically, the ability to anticipate temporal changes in the environment would enable an organism to be prepared, both physiologically and behaviorally, to perform specific activities when the environmental conditions are most favorable to the species. This confers to the organism the property of being continuously adjusted to the cyclic changes of the environment and, therefore, of being temporally adapted (Marques & Waterhouse 1994).

In non-troglobitic cavernicolous species (those which may and those which must leave the cave during their life), the presence and synchronization of endogenous rhythms would guarantee the time adjustment of exits and returns to the cave. Indeed, after Saunders (1982), studies focusing on temporal patterns with animals of each one of these categories show that activity patterns appear to reflect the relationship that each animal has with the cave. In contrast, it is generally accepted that the internal clocks of troglobites have been suppressed (Lamprecht & Weber 1991). Nevertheless, as cycles (even attenuated ones) are present in some deep regions of caves, it is possible that some rhythmic characteristics persist.

Although there are numerous troglobitic

species, few studies on biology of opilionids have been conducted (e.g., Juberthie 1964; Gnaspini 1996). We present herein information on activity rhythms and general behavior of three species of harvestmen, one troglotic and two epigean, aiming the comparison of strategies in different habitats and the contribution to the knowledge of biology of opilionids in general.

METHODS

Three species of Laniatores harvestmen (family Gonyleptidae) were used in this study. The two epigean species, *Iporangaia pustulosa* Mello-Leitão 1935 and *Iguapeia melanocephala* Mello-Leitão 1935, belong to the subfamily Progonyleptoidellinae, and the troglotic species, *Pachylospeleus strinatii* Šilhavý 1974, belongs to the monotypic subfamily Pachylospeleinae. They were chosen for two reasons. First, they are abundant and were easily available for our study. Second, one species is a restricted cave species and the others live only outside of caves. Thus, they have contrasting characteristics.

The species were collected in the Ribeira Valley, São Paulo State, southeastern Brazil. This area is a humid subtropical region without a dry season; total rainfall is 1500 mm; and the annual average temperature ranges between 17–19 °C (Setzer 1966; Monteiro 1973; see also Gnaspini 1996 for description of areas).

Recent phylogenetic analysis of the family Gonyleptidae (R. Pinto-da-Rocha, pers. comm.) has shown that Progonyleptoidellinae is the sister group of Sodreaninae + Caelopyginae. Species of this whole clade (three subfamilies) could be considered “diurnal” because they can easily be seen during the day, active or inactive. On the other hand, Pachylospeleinae belongs to a “nocturnal” clade. Epigean species of this second clade completely hide during the day, leaving their shelters only after dusk.

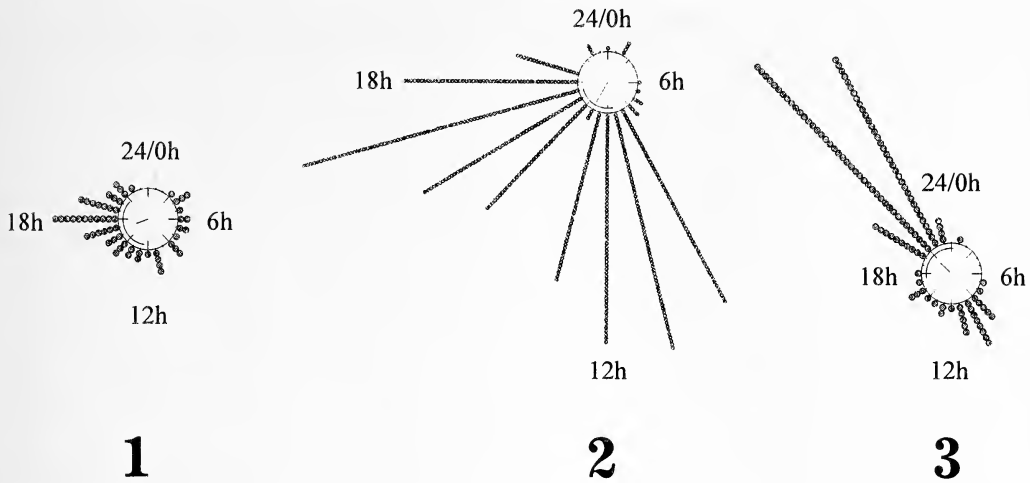
Iporangaia pustulosa and *I. melanocephala* are epigean species which live on tree trunks and on or under leaves in rainforests from southeastern Brazil. Our observations have shown that they are not gregarious species because the specimens have been always observed alone or, at most, wandering near conspecifics. Specimens of *I. pustulosa* are generally seen walking on low vegetation near

damp areas during the morning, whereas specimens of *I. melanocephala* are generally seen walking on tree trunks on the same areas. These two species were collected in the area of Parque Estadual Intervales (PEI), a mountainous region with elevation ranging from 70–1000 m (collections were made at about 800 m). Nevertheless, their geographical distribution includes the area where the third species studied is found.

The troglotic species (*P. strinatii*) was collected in the Águas Quentes cave (SP-016, elevation 180 m), located in Parque Estadual Turístico do Alto Ribeira (PETAR), at lower elevations than PEI. It is restricted to one system of caves (“Sistema das Areias”) and has been studied primarily at the population level by Pinto-da-Rocha (1996). It does not seem to be gregarious either. Its endemic distribution, allied with troglomorphisms (depigmentation and increased segmentation of tarsus of the sensorial leg II), have led Pinto-da-Rocha (1996) to consider it a troglobite. Šilhavý (1974) has also considered it a troglobite, and has added to the list of troglomorphisms the reduction of eyes. However, the species has eyes, which seem to have “normal” size.

We maintained all harvestmen species in terraria with very damp soil on the bottom. Seven individuals of *I. pustulosa* and one of *I. melanocephala* were kept under natural daylight: dark cycles, and four individuals of the cavernicolous *P. strinatii* were kept in a basement laboratory. Inside the laboratory the terraria were left in a chamber with a dark and humid environment which approximates the cave environment. All species were fed once a week with pieces of *Tenebrio obscurus* larvae. *Iporangaia pustulosa* was also fed with pieces of carrot and lettuce. During feeding, we observed behavior under natural illumination or with fluorescent bulbs.

We conducted the tests of reaction to light in a box 35 cm long with a small side retreat in the back. A glass with water provided a thermal barrier between the front of the box and an incandescent bulb (light intensity at this point = 340 lux). An individual was placed in the box 15 minutes before the test, in the end nearest the lamp (which was off) under very dim light (4 lux). During tests, the light was switched on, and the time elapsed for the animal to start walking (time of reaction) as well as the total distance walked dur-



Figures 1–3.—Results of the circular analysis of the activity rhythms of the harvestmen. 1. *Iporangaia pustulosa*; 2. *Iguapeia melanocephala*; 3. *Pachylospeleus strinatii*. The circumference represents 24 hours; each line represents the grouped data (all days recorded) of percentile activity per hour.

ing 15 minutes were recorded. Tests were conducted in different hours of the day, and, in each test, all animals have been tested at the same time. This procedure avoided both reaction differences due to endogenous timing, and differences due to specific different periods of rest/activity. The results were compared using analysis of variance (ANOVA) (Zar 1996).

Continuous records of activity rhythms were made using a system that detects vibrations and sends the data to a computer. Through acoustic sensors connected to the walls, the system recorded overall activity, by detecting all body movements of the animals, including walking, grasping and chewing the food, cleaning legs with mouth parts, etc. All records were made under continuous red light (2 lux, 680 nm), because it is well accepted among entomologists and arachnologists that this type of light does not affect the behavior of these arthropods. Moreover, previous tests showed that this light condition do not disturb the behavior of these animals. The animals were provided with food and water in the beginning of the experiment and after one week. Data were analysed using the Rayleigh test, which tests if there is a preferential direction for a circular unimodal distribution. When Rayleigh was inappropriate, the Hodges-Ajne test, which can be applied to samples with any distribution, even multimodal, was used (Zar 1996).

RESULTS

Activity rhythms.—The results of the records of activity rhythms are presented in Figs. 1–3. The circumference represents 24 h; each line represents the grouped data (all days recorded) of percentile activity per hour. Only the clearest record for each species is shown here.

The record of *I. pustulosa* was made over 7 days. The circular analysis (Fig. 1) indicates that the activity rhythm has a circadian periodicity (Rayleigh test: $R = 24.18$; $r = 0.41$; $n = 59$; $P < 0.05$; this test is more significant the closer r gets to 1.0), with the major phase of activity occurring around 1700 h. A second and much lower activity peak occurs during the morning.

The record of *I. melanocephala* continued for 11 days. The circular analysis (Fig. 2) also shows a circadian periodicity (Rayleigh test: $R = 350.43$; $r = 0.693$; $n = 506$; $P < 0.05$), with an activity peak around 1400 h.

The record of *P. strinatii* was made for 10 days. The circular analysis (Fig. 3) shows a circadian periodicity in the activity rhythm. However, the activity pattern was clearly bimodal, thus the Rayleigh test could not be applied. In order to statistically analyze these data, we utilized the test of Hodges-Ajne, that indicates a very significant circadian periodicity (Median = 21 h; $n = 120$; $m = 8$; $P < 0.05$). This means a bimodal preference for

Table 1.—Results of the reaction to light of two individuals of *Iporangaia pustulosa* and two of *Pachylospeleus strinatii*. T.R. = Time to start Reaction (min); T.D.W. = Total Distance Walked (cm). “—” represents no displacement.

Date (Time)	<i>I. pustulosa</i>				<i>P. strinatii</i>			
	ind. 1		ind. 2		ind. 1		ind. 2	
	T.R.	T.D.W.	T.R.	T.D.W.	T.R.	T.D.W.	T.R.	T.D.W.
13/Jan/98 (1000h)	4.83	10	5.38	25	2.97	257	7.5	253
16/Jan/98 (1000h)	—	—	4.833	15	12.17	41	—	—
19/Jan/98 (0400h)	1.5	18	1.9	93	0.42	203	17.8	55
22/Jan/98 (1600h)	—	—	0.5	63	1.2	184	—	—
29/Jan/98 (1400h)	—	—	7.65	27	3.6	28	10.4	27

activity at 0900 and 2100 h. The record also shows that this species walks long distances, because the activity is very intense.

Feeding behavior.—Neither the epigeal nor the cavernicolous species showed any pattern of intraspecific aggressive behavior, even when feeding occurred after a long time under starvation conditions. Instead, individuals of *I. pustulosa* stayed very close, touching each other with their sensorial legs while feeding. Even interspecific aggressiveness among *I. pustulosa*, *I. melanocephala* and *P. strinatii* was not observed. In turn, in previous observations, individuals of *Goniosoma proximum* (Mello-Leitão 1922) actually expelled *I. melanocephala* from the food (S. Hoenen, pers. obs.). The former are much larger than the latter. *G. proximum* (Goniosomatinae) can be found either in the same area where the two epigeal species occur, either in some caves. The animals studied have been collected from a granitic cave. Whether or not it is a proper cavernicolous species or if it is an accidental in caves is difficult to assure, because they may or may not inhabit caves in areas where they occur in the forest (see Gnaspini 1996 for discussion).

We observed that all epigeal tested species remove pieces of food to ingest away from the source. This movement away from the food source appears to be mediated by contact. The harvestmen seem to stop for ingestion only after they leave the area where they touch one another. This could be a behavior to avoid fighting for food among conspecifics. However, no aggressive pattern was observed when individuals casually meet each other. Moreover, this behavior occurred only when small pieces of food (e.g., pieces of beetles

and of carrot) were offered; when lettuce was offered, possibly because pieces were bigger, they ingested it in the same site, even if touching one another. Although they may rest close to each other, either intra- or interspecifically, they do not seem to be gregarious because resting close together is not the general rule. Because the animals did not exclusively retreat under shelters either before or after food capture, we do not believe that movement away from the food source is related to predator avoidance.

In contrast, this behavior of carrying food did not happen frequently in the troglolithic harvestmen. This could be related to life in an environment lacking predation pressure; the animal does not need to hide while feeding. In addition, it is probably advantageous to immediately consume food when it is patchy and scarce, like in a cave.

Reaction to light.—The results of the tests, made with two individuals of *I. pustulosa* and two of *P. strinatii*, are shown in Table 1. In order to evaluate possible differences in these responses, all values of time of reaction obtained for *I. pustulosa* were compared with those obtained for *P. strinatii* using an ANOVA. The same test was used for comparison of the total distance walked. No statistical difference concerning time of reaction was observed between the species (F-ratio = 1.670; $df = 1$; $P > 0.05$). However, there is a statistical difference for the distance walked (F-ratio = 5.514; $df = 1$; $P = 0.03$), indicating that *P. strinatii* walks for significantly greater distances than *I. pustulosa*. This is an interesting result because it suggests a greater vagility in the former species, which is an expected characteristic for a troglolite that lives in an en-

vironment with a poor food supply. Moreover, considering the apparatus used for tests with only 35 cm length, the great distances walked by *P. strinatii* implies that the animal would walk back and forth in the chamber, sometimes towards the light. This may suggest that this species has less photophobic reaction than the epigean one. However, the fact that the animals react immediately to a light source could imply reaction to a sudden stimulus, and not necessarily a photophobic reaction. We expect that any other stimulus, in addition to light (mechanic, magnetic, electric, etc.), strong enough to be detected by the animal, would promote start of activity. However, we have not tested it yet.

DISCUSSION

Both of the epigean species (*I. pustulosa* and *I. melanocephala*) show strong circadian activity rhythms, as expected facing the ubiquity of circadian clocks among surface organisms (Bünning 1967; Menna-Barreto 1997). Both species could also be characterized as "diurnal" because of the main expression of activity during the day. Accordingly, species of the whole clade that includes both *Iporangaia* and *Iguapeia* are considered "diurnal" because they are mostly seen during the day. There are two peaks for *I. pustulosa*, one after dawn and one around sunset, the latter being greater. This pattern may be explained by the temporal distribution of their "food," i.e., insects are much more available during these hours of the day, especially near sunset.

Although it is generally accepted that troglobites have lost temporal organization, at least for circadian frequencies (Lamprecht & Weber 1991), because they live in an environment without the light/dark cycle, some troglobitic species appear to maintain a circadian rhythm (e.g., Wilkens *et al.* 1990; Trajano & Menna-Barreto 1995). This is also the case of *P. strinatii*, which also shows circadian rhythmicity. This seems to be a rather intriguing result, and there are several evolutionary traits that may lead to this result. As pointed out by Husson (1971): "Cave fauna are heterogeneous, differing from one another in the age of their existence, their origins, their reactions towards environment, in the reasons for their presence in caves. On account of this heterogeneity in the cave fauna it is not reasonable to apply identical laws to all cave animals and

to hope to find the same biological rhythms." Therefore, it is not surprising that the temporal aspects of cave species, mainly the troglobites, are not as universal as those of the epigean species. The main cause for this difference is probably the diversity of ecological origins of troglobites and their adaptive characteristics (Vermeij 1987).

Our data point to an endogenous control underlying the expression of the activity of *P. strinatii*; and, although bursts of locomotion can happen at anytime, there are two main intervals within which activity seems to occur. A circadian rhythm in troglobites may be maintained either because it is advantageous, or because it is a relictual feature from an "old" epigean relationship which has not been lost. If a given troglobitic species feeds on material ruled by epigean cycle, it is expected that this species would keep circadian rhythmicity. This would apply, for example, either to a predatory troglobite which feeds on non-troglobitic organisms (which would probably show circadian rhythmicity), or to a detritivorous/scavenger/omnivorous troglobite which feeds on material which comes from the epigean environment following circadian rhythms (such as regular floods, regular wind flows). However, this does not seem to be the case for *P. strinatii*, as it seems to be mainly detritivorous/omnivorous and the input of organic material in the caves where it lives does not seem to be related to any daily event. On the other hand, the circadian rhythmicity of *P. strinatii* could be considered a relictual feature because Pachylospeleinae (which includes *Pachylospeleus*) belongs to a "nocturnal" clade, in which epigean species completely hide during the day and leave their shelters only after dusk.

Based on our data, it seems that any given stimulus, be it internal (e.g., hunger), or external (e.g., turning a light on or handling the animal), causes the start of activity of *P. strinatii*, which continues for long time intervals. This happens probably because of the scarcity of food and mates in the environment where the species lives. It is likely that, because food is patchy and scarce and should be exploited promptly, this species feeds wherever it finds food and does not take it away. In addition, the bimodal pattern of activity of *P. strinatii* may be a result of its life in the cave environment; i.e., the scarcity of food may have led

the species to look for food in a more frequent and more intensive way, causing the original nocturnal expression of the activity to become duplicate, resulting in bimodality. However, it awaits testing.

Circadian periodicities seem to be important, not only for adjustment to that habitat, but also for the maintenance of internal temporal organization (Marques *et al.* 1997), which is responsible for the regulation of different and sometimes incompatible physiological systems. Thus, an additional hypothesis is that *P. strinati* could be maintaining a circadian rhythmicity for some internal and yet unknown physiological feature.

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COURTSHIP AND MATING BEHAVIOR OF *BRACHYPELMA KLAASI* (ARANEAE, THERAPHOSIDAE)

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ABSTRACT. Courtship and mating behavior of *Brachypelma klaasi*, heretofore unknown, is described on the basis of three courtship and mating sequences, one in captivity and two in the field. Adult males perform courtship movements (pedipalp drumming, leg drumming, push-up and shaking) when they locate a female's burrow, probably in order to avoid female aggression. After some physical contact, the female raises the prosoma and extends her chelicerae. The male then grasps her chelicerae with his tibial apophyses and the female arches her body backwards leaving the epigynum exposed. The male starts boxing the female's sternum and presumably inserts his pedipalps and inseminates the female. In two cases the female vigorously attacked the male immediately after mating and probably would have killed him had observers not intervened; the other pair separated more slowly and peacefully. Males appear to use chemical and/or tactile cues from the female's silk around the burrow during short-range searching behavior. Males begin courtship behavior by drumming on the silk to signal to the female that he is present. One male of *B. klaasi* observed in the field laid silk over the female's silk around the burrow, possibly to prevent subsequent matings by other males. A second male did not detect the burrow after this act.

RESUMEN. Se describe el cortejo y apareamiento de *Brachypelma klaasi*, hasta ahora desconocidos con base en tres secuencias de cortejo y apareamiento, una en cautiverio y dos en campo. Los machos adultos realizan movimientos de cortejo (tamborileo con pedipalpos, tamborileo con patas, lagartijas y temblado) cuando localizan nidos de hembras, probablemente para evitar la agresión de las mismas. Después de un periodo de contacto físico la hembra levanta el prosoma y everta los quelíceros. El macho prende los quelíceros de la hembra con sus apófisis tibiales y la hembra se arquea hacia atrás exponiendo el epigineo. El macho boxea contra el esternón de la hembra y se asume que inserta sus pedipalpos y la insemina. En dos casos la hembra atacó al macho inmediatamente después del apareamiento y probablemente lo hubiera matado de no haber intervenido el observador, la tercera pareja se separó más lenta y pacíficamente. Apparently los machos utilizan señales químicas o táctiles de la seda de la hembra alrededor del nido durante la búsqueda de corto alcance. Los machos inician el cortejo tamborileando en la seda, probablemente para anunciar su presencia a la hembra. Un macho de *B. klaasi* observado en el campo depósito seda sobre la de la hembra alrededor del nido, posiblemente para evitar copulas subsiguientes de otros machos. Un segundo macho no pareció detectar el nido después de la conducta mencionada.

Tarantulas (Mygalomorphae, Theraphosidae) are highly diverse in Mexico, with many species distributed in restricted, endemic areas (Yáñez & Locht 1997). The genus *Brachypelma* contains nine species distributed along the Pacific coast of Mexico, eight of which have small, discrete ranges. At least one of these species, *Brachypelma klaasi* (Schmidt & Krause), and possibly more, are being considered for inclusion as endangered species under CITES.

Consequently, studies of reproductive behavior are important to aid in their reintro-

duction to their natural environment. Furthermore, few studies have been conducted on the reproductive behavior of tarantulas in general, and little of the literature that has been published contains detailed behavioral descriptions (though see Stradling 1994; Shillington & Verrell 1997). Studies that describe reproductive behavior either partially or in detail have been undertaken on the following genera: *Dugesia* (Baerg 1958; Petrunkevitch 1911), *Eurypelma* (Baerg 1928), *Cyrtopholis* (Petrunkevitch 1934), *Aphonopelma* (Bücherl 1971; Herrero & Valerio 1986; Minch 1979;

Shillington & Verrell 1997), *Grammostola* (Pérez-Miles 1988), *Ceropelma* (Pérez-Miles 1992). Here we provide a detailed description of courting and mating behavior in *Brachypelma klaasi* in the field and in captivity.

Species studied.—The female lays a single egg sac containing 400–800 eggs in her burrow in April–May. The female guards the egg sac for 2–3 months before the spiderlings emerge and disperse. In the juvenile stage, spiders produce temporary burrows until a suitable site is found for a permanent burrow which the spider inhabits for many years. Adult females reach reproductive maturity between 7–9 years and live for up to 30 years. Adult female body size ranges from 50–75 mm and female weight ranges from 19.7–50 g. Males mature earlier (between 6–8 years) and live between 4–6 months. Male weight ranges from 10–45 g (Yáñez pers. obs.).

The female's burrow varies in length from 0.15–2 m, depending on the site and the age of the spider. The burrow complex consists of a horizontal tunnel leading from the burrow entrance to a primary chamber where molting usually takes place, and an inclined tunnel that connects the primary chamber to a larger, secondary chamber where the spider rests during the night and where prey is consumed. The female puts a few silk strands at the entrance of the burrow probably so that a male can detect that a female is present. Once the male has detected the silk strands, courtship behavior may be initiated.

Brachypelma klaasi was originally placed in a new genus, *Brachypelmides*, by Schmidt & Krause (1994). However, a recent comparative study of morphology and distribution of species within *Brachypelma* provides much evidence for including *klaasi* in the *Brachypelma* group and suggests that *Brachypelmides* be used as a synonym of *Brachypelma* (Locht et al. 1999). In order to avoid confusion, we use the name *Brachypelma klaasi* (Schmidt & Krause).

METHODS

Field studies were conducted at La Estación de Biología "Chamela", Jalisco, Mexico, situated on the Pacific coast in a tropical deciduous forest (19°30'N, 105°03'W, 200 m). Courtship and mating behavior were observed in two pairs in the field on 23 November 1997. The first description of courtship and

mating (pair 1) was made at 1030 h (temperature 27 °C and 89% relative humidity) when a male (weight = 10 g) was found 4 m away from a female burrow (female weight = 40 g) and placed 10 cm in front of it in order to encourage reproductive behavior. The second description (pair 2) was made at 1700 h (temperature 27 °C and 87% relative humidity) using a male (weight = 30 g) caught several kilometers away from the second female burrow (female weight = 45 g).

A third pair (pair 3) was observed in captivity on 11 February 1998 in an environmental chamber at the Facultad de Ciencias of the National Autonomous University of Mexico in Mexico City (27 °C, 60% RH, 12:12 light cycle) using a male (weight = 27 g) caught on 24 November 1998 and a female (weight = 35 g) caught on 2 October 1997 at the field location. Prior to pairing, the male was kept isolated in a 37.5 l aquarium with soil from the collection site and small pieces of logs. The female was kept in similar conditions in a 50 l aquarium. The male was placed in the female's tank to provoke reproductive behavior.

Encounters were videotaped using a Sony HandycamTM Video 8 recorder. Video records were observed at varying speeds in order to accurately describe behavioral patterns.

RESULTS

Five behavioral patterns were observed in the male. *Pedipalp drumming* (PD): pedipalps are alternately raised and lowered, about 5 mm off the ground, each cycle lasts between 0.5–0.8 sec. *Pedipalp boxing* (PB): the male alternately strikes the female sternum with his pedipalps, each cycle lasts between 0.5–0.8 sec. Boxing cycles could not be quantified given the angle of view, since the bodies obstructed vision of ventral interactions between males and females. *Leg drumming* (LD): the two legs of the same pair are rapidly (0.1 sec) raised and lowered, between 5–20 mm off the substrate; only pairs I (LDI) or II (LDII) are involved in this pattern. *Shaking* (S): quick (< 1 sec) vibratory movements of the entire body. *Push-ups* (PU): an instantaneous raise and lowering of the body. No behavioral patterns were observed in the female, except for *shaking*, which was similar to that of the male.

Although the three reproductive events varied greatly, four stages could be defined: *Male*

approach (MA) begins when the male is placed by the observer near the female's burrow and ends when the female is observed in the entrance of the burrow. *Female response* (FR) ends when physical contact is established between male and female. *Physical contact* (PC) ends when the pair separates. *Post-mating behavior* (PM) comprises any behavior pattern performed immediately after separation.

Pair 1.—Courtship began with the male leg-drumming on the silk surrounding the burrow and shaking his body. The female came out of the burrow 64 sec after the male started drumming. As she approached, the male continued leg-drumming and drummed his pedipalps once. Female response lasted 58 sec from exiting the burrow to engaging in frontal physical contact. During physical contact, the male drummed the substrate and boxed the female, after which she arched backwards and presumably was inseminated (insemination could not be confirmed in any pair given the angle of view since the bodies obstructed vision of ventral interactions between males and females). The female then started pushing down the male, and he retreated gradually, facing her. Within a second of breaking physical contact (which lasted 84 sec) the female attacked the male vigorously, at which point the observer intervened. A drop of sperm was recovered from the female, and microscopic analysis showed a dense mass of what could be reserve substances mixed with sperm cells.

Pair 2.—The male slowly approached the burrow, frequently shaking, and entered the burrow after 261 sec, at which point the female could not be observed. They remained out of sight inside the burrow for 153 sec, after which they came out, engaged in frontal physical contact and remained like this for another 196 sec. During this period the female seemed to be highly receptive, arching the body backwards while the male boxed her, and presumably inseminated her. After a slow separation, the male started to groom his chelicerae while the female returned to the burrow. Then, 128 sec after separation, the male started to spin a thread immediately next to the female burrow for another 60 sec. A second male placed on the silk surrounding the burrow did not seem to locate the female's burrow.

Pair 3.—Immediately after being placed in-

side the female's aquarium, the male started drumming and pushing-up on silk threads spun by the female. He then approached the female from behind, at which point she turned and engaged in frontal physical contact. During physical contact, which lasted for 67 sec, the male boxed the sternum of the female though the number of bouts could not be quantified. The female pushed vigorously down on the male, an apparently aggressive act that made insemination difficult. The female then suddenly attacked the male, at which point the observer intervened. A drop of sperm was observed after separation in the left embolous palp of the male. However, insemination probably did not occur.

Of the three pairs observed, Pairs 1 and 3 displayed similar behavioral patterns compared to Pair 2 (Table 1). The female in Pair 2 was more receptive than the other females observed: the male went into her burrow and brought the female out, she arched completely during mating, and afterwards made no aggressive attempt before returning to her burrow. The other two pairs had shorter physical contact before disengaging, females arched less and pushed the male forward. In both cases the female attacked the male. The two females observed in the field, females 1 and 2, have remained within their burrows, closed with leaves and silk, to the date of submission of this paper (late April 1998) in a fashion similar to that described for other species when they are developing an egg sac (Baerg 1928).

DISCUSSION

Observations of short-range male-searching behavior suggest that males might use chemical or tactile cues from silk spun around the female's burrow. Once in contact with the female's silk, males begin courtship behavior by drumming on the silk to signal to the female that he is present. This behavior has been observed in other theraphosids (e.g., Minch 1979; Costa & Pérez-Miles 1992; Shillington & Verrell 1997). An interesting observation for one male of *B. klaasi* observed in the field was the laying down of silk over the female's silk around the burrow. It appears that this may be a method of interfering with chemical or tactile cues that may be used by subsequent males to locate the female.

Although minor differences in courtship be-

Table 1.—Duration and behavioral patterns in each stage of the three reproductive interactions observed. Abbreviations are described in the Results section, numbers are frequencies of male behavior patterns, except for FS: female *shaking*. *Pedipalp drumming* PD: pedipalps are alternately raised, about 5 mm off the ground, each cycle lasts between 0.5–0.8 seconds. *Pedipalp boxing* PB: the male alternately strikes the female sternum with his pedipalps, each cycle lasts between 0.50–0.8 seconds. *Leg drumming* LD: the two legs of the same pair are rapidly (0.1 second) raised and lowered, between 5–20 mm off the substrate; only pairs I (LDI) or II (LDII) are involved in this pattern. *Shaking* (S): quick (<1 second) vibratory movements of the entire body.

	Male approach	Female response	Physical contact	Post-mating
Pair 1 (field)	64 sec LDI:2, S:1	58 sec PD:1, LDI:5	84 sec PD:1, PB:3, LDII:3, S:1	None (female attack)
Pair 2 (field)	201 sec LDI:20, S:10	Inside female burrow (not ob- served)	196 sec PD:1, PB:2, S:6	252 sec LDI:2, S:3
Pair 3 (captivity)	153 sec PD:32, LDI:1, S:4, PU:4	116 sec S:20, PD:11, LDI: 9	67 sec PB	None (female attack)

havior were observed among the three pairs of *B. klaasi*, general aspects of the behavior were similar to those known for other theraphosid species. In particular, the “aggressive” posture adopted by the female by raising her prosoma, followed by the grasping of her chelicerae with his tibial apophyses is characteristic of many theraphosids (Baerg 1958; Minch 1979; Raven 1988; Costa & Pérez-Miles 1992; Shillington & Verrell 1997). It is worth noting that courtship behavior and mating occur outside the female’s burrow in *B. klaasi* as in other tarantula species (e.g., Costa & Pérez-Miles 1992), where there is sufficient space for the female to adopt the raised posture.

Male courting may serve various functions (Coyle 1971, 1985; Jackson & Pollard 1990; Costa & Pérez-Miles 1992; Shillington & Verrell 1997). Courting behavior by the male may inhibit female attack (Barth 1993). Aggressive female behavior towards males before, during and after mating is well known in many spider groups (Elgar 1992), as males represent a potential food resource as well as a mating opportunity for females. In the Theraphosidae, cannibalism after mating has been documented for several species (e.g., Bücherl 1951; Shillington & Verrell 1997). However, many studies have observed no sexual cannibalism (e.g., Costa & Pérez-Miles 1992; Stradling 1994), and even in species where cannibalism

has been recorded, such events are often rare (Shillington & Verrell 1997). Jackson & Pollard (1990) suggested that sexual cannibalism is generally rare in theraphosids, and that male grasping behavior may be due to factors other than avoidance of female attack. Other potential factors include communication related to mate choice (Coyle 1971, 1985), or simply as a way of maneuvering the female for successful sperm transfer (Coyle 1971; Jackson & Pollard 1990). However, low rates of sexual cannibalism in theraphosids may be a result of male grasping behavior. Without this behavior, cannibalism rates might be significantly higher. While cannibalism is rarely observed in theraphosids, aggressive female behavior directed towards the male was observed in two of the three pairs of *B. klaasi*; though whether the attacks would have resulted in cannibalism is unknown as, in both cases, the authors intervened before the male could be injured. *Brachypelma klaasi* is endemic and has small, isolated populations with limited distributions in parts of the Pacific coast (Yáñez & Loch 1998). The interactions described in this paper were staged given the rarity of the species and the difficulty of observing courtship and mating behavior under natural conditions. Compounding the rarity of *B. klaasi*, the high value placed on tarantulas in the pet trade has led to high rates of collection and trafficking of species from Mexi-

co, although the extent of trafficking in *B. klaasi* is unknown. Consequently CITES is considering giving *B. klaasi* (and other species in the *Brachypelma* group) endangered status.

Captive breeding and reintroduction of *B. klaasi* is an important means of sustaining natural populations. The studies presented here suggest that mating *B. klaasi* in captivity is not difficult and the production of eggs in the laboratory should be successful under a captive-breeding program. Furthermore, if *B. klaasi*, one of the rarest Mexican tarantulas, can be mated successfully in captivity, and studies of other species have produced similar results (e.g., Shillington & Verrell 1997) reintroductions of captive-bred individuals may be a successful technique for increasing population levels of other tarantula species.

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LOCATION OF SUCCESSFUL STRIKES ON PREY BY JUVENILE CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

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ABSTRACT. Second-instar crab spiderlings *Misumena vatia* (ca. 0.6 mg) that had never previously fed made killing attacks on pomace flies *Drosophila melanogaster* (ca. 1.0 mg) in direct proportion to the surface areas of the flies' body parts: abdomen, 50%; thorax, 29%; head, 20%. They retained this pattern over their next six encounters with these flies. They also attacked the different surfaces of these body parts (front, side, above, below, behind) with a frequency predicted by the respective areas of these surfaces. All of the spiderlings tested more than once successfully attacked prey on more than one body part. Fifth and sixth-instar *Misumena* (ca. 7–15 mg) attacked small (4 mg) syrphid flies *Toxomerus marginatus* more frequently on the head than the second instars attacked *Drosophila* heads. This difference may result from subsequent experience, greater activity of the syrphid flies than the *Drosophila*, or maturation of the spiders.

A wide variety of animals employ a sit-and-wait predatory strategy, ranging from spiders and insects to lions (Curio 1976; Morse 1980). Sit-and-wait predators depend primarily on prey coming to them and consequently will encounter many of these prey either head-on or tangentially, even though some of these predators may orient to their prey and even pursue them for short distances. These predators often increase their proficiency with experience (Bailey 1985; Cloarec 1991), which may result from the development and refinement of a particular repertoire (Papaj & Prokopy 1989), and may include new prey species as the predator grows, or as the season changes (e.g., Erickson & Morse 1997). The body part (head, thorax, abdomen) of the prey struck by the predator may form an important part of a developing repertoire exhibited by sit-and-wait predators.

Little information exists on the initial part of the body struck successfully by spiders, including classic sit-and-wait predators (Foelix 1996a, 1996b), despite the oft-cited “neck-bites” found in general sources (e.g., Bristowe 1958; Main 1976). To my knowledge, information on strike sites does not exist for naive spiderlings of any species making their first kill. Spiderlings are excellent subjects for such an investigation, because they can be easily obtained in large numbers and can be easily run in enclosures using readily available prey.

In this paper I report the body parts of prey, wild-type pomace flies *Drosophila melanogaster* Meigen, successfully struck by just-emerged, second-instar crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae) making their first captures, as well as the body parts successfully attacked in several subsequent captures by these spiderlings. *Drosophila* approximate the size and activity patterns of small Diptera encountered by the spiderlings in the field and often constituting their first captures (Morse 1993). I then compare these results with those of fifth and sixth-instar *Misumena* attacking small syrphid flies *Toxomerus marginatus* (Say), an important prey item of older *Misumena* in the field. These results provide important insights into the development of prey-capture behavior in *Misumena* and also provide the basis for future comparisons with other species.

METHODS

I obtained all spiders and syrphid flies from old fields and roadsides in South Bristol, Lincoln County, Maine in August of 1995 and 1996, and *Drosophila* came from wild-type laboratory stocks. All second-instar spiderlings used in this study had emerged from their egg sacs within the preceding two days at the time of their first observation. The egg sacs themselves had been collected from the field shortly before emergence. Laying dates

of these clutches were known, so approximate emergence dates could be calculated. Middle-instar spiders and syrphid flies were collected from goldenrod (*Solidago* spp.) flowers, which both the spiders and the flies frequented during August. All spiderlings were weighed before their first experimental run, and their similar masses (0.4–0.7 mg; Morse 1993) ensured that they had not cannibalized their sibs [a rare event occurring in less than 10% of the broods (DHM unpubl. data)], and, therefore, had not previously fed. The spiderlings were tested seven times, at three-day intervals. Since a few were lost during handling, a few died, and most refused to feed on one or more occasions, I obtained the maximum seven data points for only four of the 32 individuals run in this protocol.

I placed approximately 10 *Drosophila* (ca. 1.0 mg, 3 mm body length) in a petri dish (6 cm diameter) and then added a second-instar spiderling to the dish. Although a high-density setting, this density is frequently approximated when just-emerged, second-instar *Misumena* recruit onto goldenrod inflorescences that contained large numbers of small dance flies (Empididae) (Morse 1993). The *Drosophila* were lightly chilled to immobilize them sufficiently for convenient handling, and then allowed to recover before adding the spiderling. I recorded the body part where the spiders first successfully struck their prey (head, thorax, abdomen) and the surface of the body part they struck (anterior, lateral, dorsal, ventral, and posterior). As soon as a spiderling captured either a *Drosophila* or syrphid fly, I viewed it under a dissecting microscope to verify the site of the successful attack. Since these individuals were carefully observed for up to 30 min, I missed few predation events. The close observations ensured that none of the spiderlings shifted their positions on their prey before being recorded. Spiders often reposition their prey subsequent to capture (Foeelix 1996a), necessitating this close attention. These spiderlings required a few minutes to shift from the original kill site (pers. obs.), although attention to obtaining original kill sites made it impossible to record exact shift times as well.

I calculated expected frequencies of attacks on the head, thorax, and abdomen as the relative surface area of each of these body parts; excluding the posterior surface of the head,

anterior and posterior surfaces of the thorax and anterior surface of the abdomen; surfaces largely occluded from strikes by surrounding structures. I calculated the areas from measurements of length and width of the head and thorax, estimating them to be cylinders. The anterior surface of the head was calculated as the area of a circle. The anterior part of the abdomen, back to the point at which it tapered, was also treated as a cylinder, and the remaining posterior part as a cone. This calculation assumed that the spaces separating head and thorax, and the thorax and abdomen, were too narrow to permit a successful strike and deleted these surfaces from the areas calculated. Since only four of 148 successful attacks struck these sites between the body parts, the criteria seem appropriate.

I also gathered similar data on the prey capture of small (ca. 4.0 mg, 5 mm; Morse 1979, 1998) syrphid flies *Toxomerus marginatus* by older, wild-caught, juvenile female *Misumena* weighing 6.9–15.6 mg (probably fifth and sixth instars). Relative proportions of area on the three body parts of *Toxomerus* were calculated as for *Drosophila*. These observations were made in 7-dram vials (5 cm long, 3 cm diameter), which also permitted me to observe initial capture sites. However, I did not record the part of the head, thorax, or abdomen where the syrphids were struck by the spiders.

RESULTS

Second instars attacking *Drosophila*.—In their first run, naive second instars made more of their first killing attacks to the abdomen than to the thorax or head of *Drosophila*, and more killing attacks to the thorax than to the head (abdomen > thorax > head) (Table 1). This distribution of killing attacks to the different body parts did not differ significantly from the number predicted as a consequence of the different surface areas of these body parts (Table 1) ($G = 1.09$, $df = 2$, $P > 0.5$ in a G -test), since the surface area of the abdomen considerably exceeded that of the thorax, which in turn exceeded that of the head (Table 1). Likewise, the sites of attack in the original trial and in the mean of the combined subsequent trials did not differ (Table 1) ($G = 0.36$, $df = 2$, $P > 0.8$ in a G -test). Neither did the original and last trials (Table 1) differ in a G -test ($G = 0.90$, $df = 2$, $P > 0.5$). In fact, comparisons of only two pairs of trials (2 and

Table 1.—Successful strikes (kills) of *Misumena vatia* on body parts of prey and percentage of total surface area of each body part. Predicted number of strikes (in parentheses), based on percentage of total surface area.

	Head	Thorax	Abdomen
<i>Drosophila</i> strikes			
First run	5 (4.4)	7 (6.9)	12 (12.7)
Second run	3 (5.4)	10 (8.3)	16 (15.3)
Third run	4 (5.2)	14 (8.0)	10 (14.8)
Fourth run	7 (3.9)	5 (6.0)	9 (11.1)
Fifth run	5 (3.2)	6 (4.8)	6 (9.0)
Sixth run	6 (2.0)	2 (3.2)	3 (5.8)
Seventh run	6 (3.3)	5 (5.2)	7 (9.5)
% surface area	18.6	28.6	52.8
<i>Toxomerus</i> strikes			
First run	15 (5.8)	12 (8.9)	4 (16.3)
% surface area	17.5	28.2	54.3

6, 3 and 6) differed at $P < 0.05$ (2 vs. 6: $G = 8.21$, $df = 2$, $P < 0.02$ in G -test; 3 vs. 6: $G = 6.84$, $df = 2$, $P < 0.05$ in same test), and their validity is highly suspect, because of the small sample sizes in two cells of Trial 6. Further, neither comparison is significant when a sequential Bonferroni adjustment (Rice 1989) is applied to accommodate for the multiple comparisons carried out. Successful strikes in runs 2–7 continued to follow the order abdomen > thorax > head in most instances, consistent with the different surface areas of the three body parts. Thus, no significant shift in sites occurred over the period during which these spiderlings killed their first several prey.

None of the spiderlings specialized strongly on a particular body part; in fact, none of the 29 individuals tested more than once confined their kills to a single body part ($P < 0.001$ in a binomial test). The pattern of attack thus showed little sign of specialization, at the individual or population level.

Table 2.—Strikes of second-instar *Misumena vatia* on different surfaces of *Drosophila* body parts. Predicted number of strikes in parentheses, based on percentage of total surface area.

Body part	Surface area				
	Front	Side	Above	Below	Behind
Head	12 (8.4)	8 (9.2)	4 (4.6)	9 (4.6)	3 —
Thorax	0 —	24 (20.5)	9 (10.3)	15 (10.3)	1 —
Abdomen	0 —	19 (27.8)	9 (13.9)	22 (13.9)	13 (20.5)

As no clear shifts in killing patterns emerged in the analysis of consecutive kills, I pooled the data from the different runs in order to establish how the spiderlings directed their killing attacks to the different surfaces of the body parts (Table 2). With 15 total surfaces recognized (Table 2), the sample of kills from any single run or pair of runs was not large enough to test statistically. The results can, however, establish where a predator most frequently attacks a prey species, an aspect that may serve to drive selection of prey-capture techniques of the predator, and corresponding selection on the prey species.

The spiderlings showed little tendency to capture prey by striking between the body parts, with only four such successful strikes, these being directed to the rear of the head (3) and the rear of the thorax (1). Deleting the areas of these four surfaces largely covered by adjacent body parts, successful attacks were carried out to the 11 remaining surfaces of the three body parts at rates that did not differ from the predicted ($G = 10.81$, $df = 10$, $P > 0.3$ in a one-sample G -test). Thus, the areas of the various surfaces of the different body parts also accurately predicted the rates at which these sites were successfully struck.

Later instars attacking syrphid flies.—Middle-instar spiders successfully struck *Toxomerus* on the head and thorax far more often than predicted by chance, based on the respective surface areas of the body parts (Table 1) ($G = 31.13$, $df = 2$, $P < 0.001$ in a G -test). This tendency differed significantly from that of the second instars capturing their first prey item ($G = 12.42$, $df = 2$, $P < 0.01$ in a G -test). I did not record the surfaces of the body parts struck that resulted in kills by these middle-instar spiders.

DISCUSSION

These spiders must be able to capture a broad range of prey over their lifetimes, both

as a consequence of their change in size and with the progression of the season. Opportunities will also differ with the habitat, and these sit-and-wait predators will also experience changes associated with the flower hunting sites experienced here. It is thus not surprising that the spiderlings do not exhibit a highly programmed repertoire upon initial experience with prey. Species with such varied demands often learn to perfect foraging repertoires appropriate to their context; where parental care is involved, this procedure often involves extensive information passed on from parent to offspring (e.g., Altmann 1998); where not, extensive trial-and-error may be required (e.g., Heinrich 1976).

It is of interest that the spiderlings did not exhibit any clear pattern of change in surfaces struck over seven runs. Clearly, they caught these prey with little difficulty, mostly capturing a *Drosophila* in a few seconds to several minutes (DHM pers. obs.), and thus they probably never accumulated information that favored shifts in prey-capture patterns. These spiderlings' high success rates differ markedly from that of second instars attacking *Toxomerus* flies (Erickson & Morse 1997), or that of adults on bumble bees *Bombus* spp. (Fritz & Morse 1985), both far more formidable prey than *Drosophila*. Although the conditions experienced in this experiment clearly differ from many situations experienced by novice foragers, such conditions are not unusual for naive *Misumena* spiderlings, as they typically recruit onto goldenrod inflorescences, which have wide, platform-like surfaces and, often, dozens of dance flies of 0.7–0.8 mg mass within a single small group of inflorescences. These flies are slow-moving and show little sign of responding evasively to the spiderlings (Morse 1993), and spiderlings probably experience little selection to position their site of attack more precisely on these small prey.

The tendency of the spiderlings to approximate predictions of strike sites based on surface areas of the prey, and the stronger orientation to the anterior part of the body in the larger spiders, suggest that the spiders modify their patterns somewhat with experience, although maturation could also account for the change. The failure of spiderlings to confine their activities to one body part or another may simply be a consequence of the substan-

tial proportions of prey taking trajectories that place them both face-on and lateral to the spiders, as occurs routinely when foraging on flowers in the field (Morse 1986). The older spiders probably also encounter higher proportions of prey moving directly toward them, as frequently occurs with active prey (Curio 1976), which would further enhance the probability of striking the anterior parts of a prey item. Although the spiders attacked these flies in laboratory containers rather than on flowers, the frequency in the field seems unlikely to change greatly because of the spiders' primary foraging strategy of waiting for such insects to approach them.

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SAMPLING METHOD AND TIME DETERMINES COMPOSITION OF SPIDER COLLECTIONS

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ABSTRACT. Sampling methods and times can misrepresent components of spider assemblages found in tree crops. I collected 2561 spiders, including 20 families, 77 genera and 140 species, from inland and coastal south-east Queensland citrus orchards maintained under Integrated Pest Management programs. Spider assemblages, collected diurnally and nocturnally using vacuum and pit-trap sampling methods over four seasonal periods (spring, summer, autumn and winter), were compared using Simpson and Shannon-Wiener diversity indices and Morisita-Horn similarity index. Significantly different spider assemblages were collected by the two sampling methods in all orchards and seasons. Nocturnal and diurnal sample data differed for spider abundance (similarity) and diversity for several orchards. These results indicate the need to conduct nocturnal and diurnal sampling using a combination of sampling methods to reduce misinterpretation of the composition of spider assemblages. Such misinterpretations may underestimate the predatory importance of spiders in agricultural ecosystems.

Spiders are gaining favor in ecological studies as indicators of environmental quality (Clausen 1986; Maelfert et al. 1990; Churchill 1997), and as biological control agents in agricultural ecosystems (Riechert & Lockley 1984; Young & Lockley 1985; Nyffeler & Benz 1987; Bishop & Riechert 1990). Knowledge of field populations of spiders, and the sampling techniques for gaining that knowledge, are therefore of great importance.

Different collecting methods can misrepresent certain components of spider assemblages (Merrett & Snazell 1983; Churchill 1993). For instance, pitfall traps, which are commonly used for spider collecting, are effective for ground-dwelling spiders but underestimate the diversity and abundance of the foliage-dwelling fauna. Many surveys of spiders in agricultural ecosystems employ pit-traps alone (Alderweireldt & Desender 1990; Vangsgaard et al. 1990). Canopy fogging (Basset 1990; Russell-Smith & Stork 1995) underestimates web-building and web-producing spiders which can remain attached to their webs or suspended in foliage after the insecticide treatment. Branch beating can under-represent web-building spiders. For instance, *Neoscona oxacensis* (Keyserling) did not constitute a high percentage of spiders collected by branch-beating in vineyards, although the webs and spiders were numerous and highly

visible between rows of vines (Costello & Daane 1995).

Fewer spiders were collected by vacuum sampling than pitfall trapping in heathland (Merrett 1983). Fogging is not an option in orchards under Integrated Pest Management as imported biological control insects may be unnecessarily destroyed, and branch-beating at night is not successful as escaping spiders are not easily seen in poor light (Green unpubl. data). Consequently, vacuum suction, in conjunction with pit-fall trapping, is chosen for this study. Merrett & Snazell (1983) recommend a combination of vacuum and pit-trapping for sampling spiders in heathland and De Barro (1991) advocates the use of a two stroke gasoline-driven blower vacuum for aphids on wheat.

The temporal dimension to spider foraging behavior must also be considered. Diurnal and nocturnal sampling appear necessary to effectively sample all of the spider fauna as many spiders are nocturnal (Coddington et al. 1990). Most studies which use several methods, such as hand collecting, sweep nets or vacuum samples, are usually conducted during daylight hours (Young & Lockley 1990; Mason 1992; Breene et al. 1993a, b). Some studies include nocturnal samples or observations of spider assemblages (Coddington et al. 1990; Coddington et al. 1996; Dobyns 1997).

Sampling methods should be kept to a mini-

num to reduce complexity in the sampling protocol, and methods chosen should minimize species overlap by collecting different spider assemblages (Coddington et al. 1990). Here I demonstrate the importance of a combination of two sampling methods, in this case vacuum and pit-trap, and sampling times, diurnal and nocturnal, for determining the numerically abundant spider species in citrus orchards.

STUDY AREA AND METHODS

Study locations.—Spiders were collected from two inland (Mundubbera 25°35'S, 151°18'E, 300 km from the coast) and two coastal (Coochin Creek 26°54'S, 153°05'E) citrus orchards in south-east Queensland, Australia; the orchards are under an Integrated Pest Management (IPM) program which has been developed around biological control and the limited use of pesticides. Consequently, higher numbers of native natural enemies like spiders are conserved than in chemically managed orchards. Sampling was conducted diurnally and nocturnally over four seasons from Spring 1993 to Winter 1994. Sampling took place over the middle month of each season. Replicates in each orchard were sampled once per season. Sampling occurred under suitable weather conditions for spider collection, temperatures between 5–38 °C and no rain. Ellendale mandarins and Navel oranges from inland orchards, and Valencia and Navel oranges from the coastal orchards were sampled.

Sampling methods.—Four groups of six trees each were randomly selected in each orchard in each season, giving a total of 24 trees sampled per orchard per season. Within each group of six trees, three trees were sampled diurnally and three were sampled nocturnally. Vacuum-sampling was carried out for 15 minutes per tree between 0630–1030 h for diurnal samples and between 1800–2200 h for nocturnal samples. Nocturnal sampling was effected by wearing a headlamp. Foliage, trunk and branches were sampled on each tree to the height of the author's reach plus the length of the sampler (about 2.5 m).

A Little Wonder Power Blower™ (Model 9444E, Korditz, Japan) powered by a two-stroke gasoline motor was used for suction sampling. The only modification, a net sleeve, was placed inside the muzzle of the vacuum

to facilitate spider collection. After suction sampling, spiders were placed into labelled killing jars containing ethyl acetate before being transferred, in the laboratory, to labelled glass vials containing 70% EtOH.

Pit-traps consisted of plastic food containers (115 mm diameter, 80 mm deep) which were three-quarters filled with detergent and water (1:40). The traps were placed in the ground, so that the soil was flush with the rim, one trap under each of three trees (about 7.3 m apart) in each block of six trees. The containers were left open for one week. Specimens collected from pit-traps were placed into labelled glass vials containing 70% alcohol.

Data analysis.—Diversity analysis, using 10,000 randomizations, determined the significance of observed differences in community structure between two sampling methods and two sampling times based on species abundance distributions (Solow 1993). Two diversity indices used are the Shannon-Wiener index, which is sensitive to changes in the abundance of rare species in a community, and the Simpson index, which is sensitive to changes in the most abundant species in a community (Solow 1993). Shannon-Wiener index, which increases with the number of species in the community, is an ordinal scale. An index of 2 does not suggest that community is twice as diverse as a community with an index of 1. The values for Simpson's index vary between 0 (for a sample with high diversity) and 1 (for a sample dominated by a few species) (Solow 1993). Shannon-Wiener index is defined as:

$$H = -\sum_i p_i \log p_i$$

where: p_i = the observed relative abundance of a particular species (Solow 1993). Simpson index is defined as:

$$D = \frac{\sum n_i(n_i - 1)}{[N(N - 1)]}$$

where: n_i = the number of individuals of species i , and $N = \sum n_i$ (Solow 1993). Two-tailed tests were used to test the hypotheses that the two sampling methods (pit-trapping and vacuum sampling) and sampling at different times of the day (diurnal and nocturnal) collect different abundance and composition of spider assemblages.

The Morisita-Horn index (Wolda 1981; Krebs 1989) was used to calculate similarity

Table 1.—Shannon-Wiener (H) and Simpson (D) diversity indices and Morisita-Horn similarity indices (MH) for vacuum and pit-trap samples in three IPM orchards during four seasons. *n* = total number of genera collected by each sampling method; Diff. = difference between diversity indices for vacuum and pit-trap sampling methods.

Season	Orchard	<i>n</i>		H		Diff.	D		Diff.	MH
		Pit	Vac	Pit	Vac		Pit	Vac		
Summer	Coastal	1	14	0.00	2.16	−2.16	1.00	0.18	0.82	0.000
	Inland 1	4	25	0.93	2.17	−1.24	0.51	0.18	0.33	0.004
	Inland 2	6	31	0.57	2.38	−1.81	0.77	0.20	0.57	0.002
Autumn	Coastal	4	26	0.63	2.36	−1.73	0.69	0.18	0.51	0.003
	Inland 1	6	17	1.26	2.58	−1.32	0.41	0.09	0.32	0.010
	Inland 2	6	28	0.38	2.62	−2.24	0.86	0.11	0.75	0.000
Winter	Coastal	2	22	0.44	2.81	−2.37	0.73	0.07	0.65	0.000
	Inland 1	3	18	0.60	2.00	−1.40	0.68	0.25	0.43	0.003
	Inland 2	4	20	0.56	2.52	−1.97	0.75	0.11	0.64	0.013
Spring	Coastal	5	25	1.23	2.33	−1.11	0.35	0.15	0.20	0.000
	Inland 1	7	24	1.18	2.65	−1.47	0.41	0.09	0.32	0.008
	Inland 2	6	43	1.09	2.80	−1.71	0.47	0.09	0.38	0.106

(or non-similarity) between spider populations from two sampling methods and two sampling times. The index is independent of sample size and diversity (Wolda 1981) and is an appropriate measure to compare community structure in day and night sampling using vacuum and pit-trap sampling methods. The Morisita-Horn index was calculated from:

$$MH = \frac{2 \sum n_{ij} n_{ik}}{(\lambda_1 + \lambda_2) N_1 N_2}$$

where MH = Morisita-Horn index of similarity between sampling methods *j* and *k*, *n_{ij}* = the number of individuals of species *i* in sample *j*, *N₁* = the total number of individuals of all species in sample *j*, and *λ₁* =

$$\frac{\sum N_{1i}^2}{N_1^2}$$

Diversity and similarity indices were achieved using spider abundance at the genus level to minimize false results from rare species. This study is part of a larger project which investigated the potential of spiders as natural pest control agents in citrus orchards in south-east Queensland.

RESULTS

I collected a total of 2561 spiders, including 20 families, 77 genera and 140 species. All spiders, including immatures (29%), were identified to genus or species with the help of Dr. Robert Raven, Queensland Museum.

Effect of sampling method.—For each orchard in each season, diversity indices for genera differed significantly between vacuum sampling and pit-trapping using either Shannon-Wiener (H) or Simpson (D) analyses (*P* < 0.0001, Table 1). Differences were also apparent at family and species level (Table 1). Similarity values differed markedly for each orchard in each season; all values were below 0.01 (Table 2).

Generic composition was markedly different for each sampling method. Only 13 species (10%), 13 genera (18%) and 8 families (40%) were common to both methods. Combined data for all orchards in all seasons showed that at all taxonomic levels, more taxa were collected by vacuum sampling than by pit-traps (Fig. 1A). No lycosids or zodariids, and few gnaphosids and corinnids, were collected by vacuum sampling. Spiders from these families are ground-dwelling spiders. Some salticids were collected in pit-traps but the vast majority were found in the upper stratification of the orchard. Different spider communities were seen in the orchard for the two main stratification layers—trees (81–97% of total taxa) and ground (29–57% of total taxa).

Effect of sampling time.—Pit-traps were left open for one week continuously; consequently these data are not included in the diurnal/nocturnal analysis. Generic richness was significantly different between diurnal and

Table 2.—Shannon-Wiener (H) and Simpson (D) diversity indices, their *P*-values, and Morisita-Horn similarity indices (MH) for diurnal and nocturnal samples in three IPM orchards during four seasons. *n* = total number of genera collected in each time period; Diff = difference between diversity indices for diurnal and nocturnal sampling periods.

Season	Orchard	<i>n</i>		H		Diff.	<i>P</i>	D		Diff.	<i>P</i>	MH
		AM	PM	AM	PM			AM	PM			
Summer	Coastal	6	10	1.42	2.02	−0.6	<0.0001	0.32	0.17	0.15	<0.0001	0.645
	Inland 1	17	19	1.95	2.46	−0.51	<0.0001	0.21	0.13	0.08	<0.0001	0.748
	Inland 2	23	22	2.26	2.24	−0.02	<0.7	0.19	0.21	0.02	<0.0001	0.963
Autumn	Coastal	18	17	2.15	2.08	0.07	<0.3	0.18	0.22	−0.03	<0.0001	0.869
	Inland 1	15	10	2.12	2.46	−0.34	<0.001	0.13	0.09	0.04	<0.0004	0.510
	Inland 2	21	21	2.42	2.36	0.06	<0.3	0.14	0.14	−0.004	<0.5	0.821
Winter	Coastal	15	15	2.54	2.56	−0.02	<0.7	0.09	0.08	0.004	<0.6	0.663
	Inland 1	14	14	1.94	1.91	0.04	<0.4	0.25	0.25	−0.009	<0.06	0.983
	Inland 2	14	17	2.35	2.43	−0.07	<0.2	0.12	0.12	0.003	<0.6	0.825
Spring	Coastal	21	22	2.56	2.61	−0.04	<0.5	0.10	−0.11	−0.01	<0.7	0.912
	Inland 1	18	19	2.48	1.5	0.99	<0.0001	0.11	−0.42	−0.31	<0.0001	0.283
	Inland 2	24	24	2.56	2.48	0.08	<0.05	0.10	−0.11	−0.01	<0.01	0.701

nocturnal sampling in 42% (Shannon-Wiener) and 58% (Simpson) of samples over four seasons (*P* < 0.05) (Table 2). Although Shannon-Wiener indices for diurnal and nocturnal collections from two orchards (Summer Inland 2, Autumn Coastal) showed no difference (*P* < 0.3), Simpson indices were significantly different (*P* < 0.05). Numerical dominance by some species (i.e., *Zenodorus orbiculatus* (Keyserling), Salticidae, and *Cyrtophora moluccensis* Doleschall, Araneidae) was considerably higher in diurnal than nocturnal samples in Summer Inland 2, while dominance varied between diurnal and nocturnal collections in Autumn Coastal. The sensitivity to dominance of the Simpson's index may account for this result. Inland 1 showed significant differences between the two collection times in all seasons (Table 2). Greater numbers of spiders collected in the warmer months provide a possible explanation for greater differences in species richness in Summer, Spring and Autumn than in Winter (Table 2).

Morisita-Horn similarity indices (MH) for diurnal and nocturnal sampling were relatively high in comparison with those for sampling methods. Most MH values for sampling times corresponded with the diversity indices, i.e., similar MH, similar H and D (Table 2). However, while MH and D for Summer Inland 2 showed similarity between the two sampling times, H showed a significant difference. Nine rare species (i.e., < 2 individuals collected)

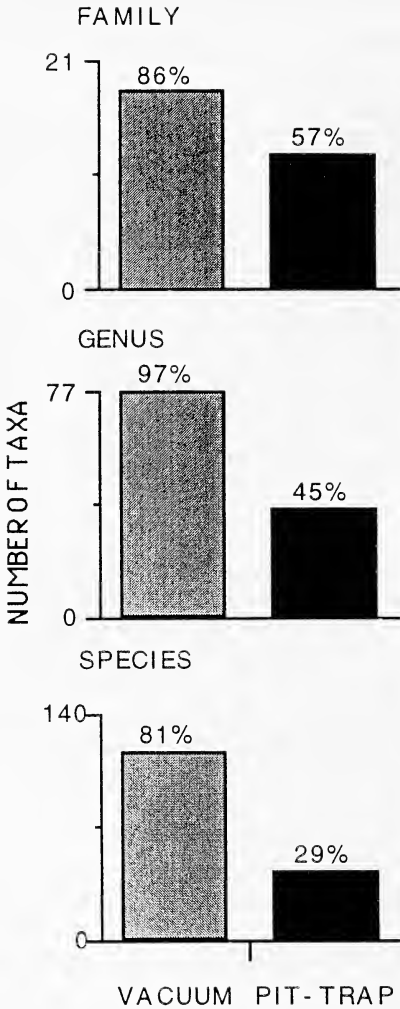
which were not common to both times were collected in this orchard; the significant difference between the two sampling times is a result of the Shannon-Wiener sensitivity to rare species.

Most families were included in collections at both sampling times. Nocturnal spiders, like *Eriophora transmarina*, the clubionid *Cheiracanthium* sp. 'a', and *Heteropoda* sp. 'a', were collected in greater numbers at night than in the day time. Families collected only at night were Deinopidae, Gnaphosidae, Lamponidae and Mimetidae. Combined vacuum data for each orchard in each location in each season show 57–75% of taxa were collected diurnally; 69–87% were collected nocturnally (Figure 1B).

DISCUSSION

Effect of sampling method.—In contrast to this study, pitfall traps collected more spider taxa in heathland than sweep-netting and visual searching (Churchill 1993) or vacuum sampling (Merrett & Snazell 1983). Vegetational architecture plays a major role in the species composition found within a habitat (Scheidler 1990), and vegetation which is structurally more complex can sustain a higher abundance and diversity of spiders (Hatley & MacMahon 1980). Diversity in web-building spiders is significantly correlated with vegetation height (Greenstone 1984) and high species diversity in wandering ground-dwell-

A



B

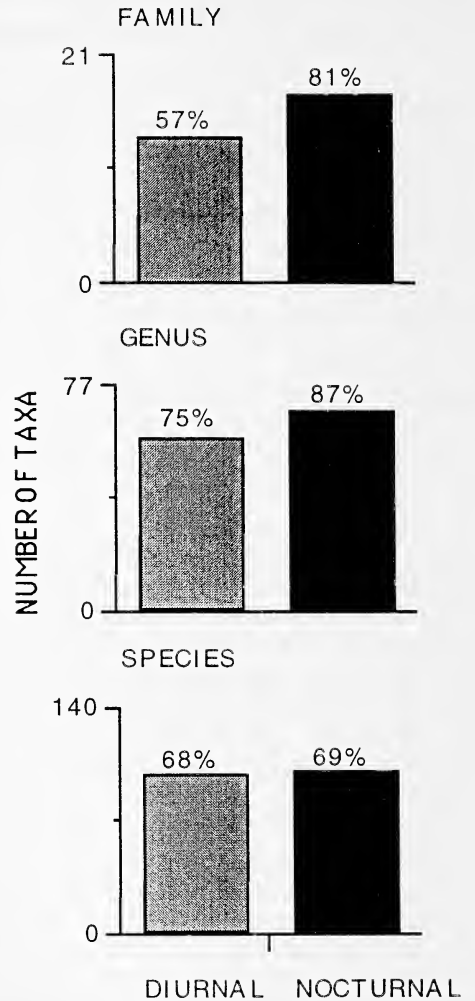


Figure 1.—(A). Total number of taxa caught by vacuum and pit-trap sampling methods (Percentages are of total taxa collected). (B). Total number of taxa caught by diurnal and nocturnal sampling (Percentages are of total vacuum samples—pit-trap data are not included in this analysis).

ing spiders is correlated with large amounts of litter (Uetz 1975; Koch & Majer 1980). The low shrubs and abundant ground cover in Tasmanian heathland (Churchill 1995) differ markedly from the mature (> 2 m high) citrus trees with little understorey. Differences in vegetational architecture at the two sites account for the different community structures seen in foliage and ground-dwelling spiders.

Effect of sampling time.—Although other studies included observation or sampling of nocturnal species, for various reasons such as results were not quantified (Provencher et al.

1988) or results were combined (Costello & Daane 1995), these studies could not be compared with the present study in terms of differences in species diversity, abundance or similarity between nocturnal and diurnal collections.

Coddington et al. (1996) found time of day had no significant bearing on the taxonomic composition of the samples from temperate forests. However, these authors recommend both day and night collecting to maximize the species richness of the samples. In the same temperate forest, abundance of adult spiders

differed significantly between day and night samples, but similarity indices were similar for the two time periods (Dobyns 1997). Tropical forests produced significantly more species in nocturnal samples than the temperate forests (Coddington et al. 1991). This agrees with the present study which was conducted in sub-tropical citrus, suggesting that species differences are greater in tropical forests than in temperate forests and, consequently, that nocturnal predation is higher in sub-tropical and tropical zones.

Sampling times and methods showed different profiles at the family level in spider assemblages. Similarity (MH) indices for differences in sampling times did not all show differences in abundance. However, the results demonstrate the need for different sampling times to provide a more extensive estimate of spider diversity and abundance. Spiders from 4 of 21 families were collected only nocturnally. Had sampling been limited to daylight hours these families would not have been included in the overall composition of the spider assemblage.

In conclusion, this study has established that a combination of sampling methods over two time periods, diurnal and nocturnal, is essential for a comprehensive assessment of the spider fauna to be made, particularly in sub-tropical areas. The vegetational architecture of a habitat must be taken into consideration before sampling commences. Each sampling method was oriented to different strata of the vegetation and so spiders with contrasting foraging behavior and habitats were collected. Vacuum sampling collected considerably more representatives of each taxonomic level but missed one group of hunting spiders, the ground-dwellers. Pit-trapping is necessary to collect these spiders.

This research has important ramifications in terms of assessing biodiversity of native natural enemies in agricultural ecosystems for pest management, and sampling agricultural crops in general to provide a greater understanding of the composition of all invertebrate fauna including pests and beneficials. A combination of vacuum sampling and pit-trapping, used diurnally and nocturnally is recommended for spider collection in tropical or sub-tropical orchards to sample a greater percentage of the spider fauna.

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NOTES ON THE BIOGEOGRAPHY AND NATURAL HISTORY OF THE ORBWEAVING SPIDER *CAREPALXIS* (ARANEAE, ARANEIDAE), INCLUDING A GUMNUT MIMIC FROM SOUTHWESTERN AUSTRALIA

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ABSTRACT. The biogeography of the Gondwanan orbweaving spider *Carepalxis* is reviewed. The genus occurs in Central and northern South America, Australia and New Guinea. It is recorded for the first time from Western Australia. Mimicry of a gumnut (eucalypt seed capsule) is described and illustrated for a southwestern Australian species. It is postulated that the mimicry protects the spiders from bird predation.

The Australian spider fauna includes a significant Gondwanan component. Even amongst taxonomically rich, cosmopolitan families such as the Araneidae, there are some genera with characteristic Gondwanan geographic ranges. The orbweaving genera *Pararaneus* Caporiacco 1940 and *Carepalxis* L. Koch 1872 are examples. *Pararaneus* (like the mygalomorph Paramiginae) is distributed in Africa and Australia where it is possibly confined to southwestern Western Australia (Main unpubl. data). *Carepalxis* (as with the mygalomorph Actinopodidae, Goloboff & Platnick 1987) occurs in Central and South America and Australia (Levi 1992; Bonnet 1956; Roewer 1942) and New Guinea (Chrysanthus 1961; Brignoli 1983).

Within Australia, *Carepalxis* has been recorded previously only from eastern Australia. Some years ago in southwestern Australia I observed an interesting specimen of *Carepalxis* which appeared to mimic a gumnut (seed capsule of a eucalypt) and this aroused my interest in the genus. Prior to this and more recently the Western Australian Museum has acquired a small collection of specimens of *Carepalxis* comprised of several species from widely scattered localities in Western Australia.

This paper presents preliminary remarks on the systematics and biogeography of Australian *Carepalxis* species, records for the first time the occurrence of the genus in Western Australia, and describes the natural history

and the apparent mimicry of a southwestern Australian species.

SYSTEMATICS AND BIOGEOGRAPHY

Carepalxis L. Koch

Carepalxis L. Koch 1872: 123. Type species by monotypy *C. montifera* L. Koch 1872: 123. Holotype female from Mackay, Queensland, Australia, originally in Godeffroy Museum, now in Zoologisches Institut und Museum, Hamburg (not examined). *Carepalxis*: Davies 1988: 300, Pl. 22. *Carepalxis*: Levi 1992: 252.

See also Bonnet (1956), Roewer (1942) and Brignoli (1983) for species lists and synonyms.

Comments.—Levi examined the type of *montifera* and reported that it has a shrivelled abdomen and that the scape of the epigynum was torn off (Levi 1992). Davies (1988) illustrated a specimen, including the epigynum, which she identified as *C. tuberculata* Keyserling.

Diagnostic notes.—The most characteristic feature of *Carepalxis* is the pair of large humps on the carapace of the female. These have the appearance of two subdued horns (see Davies 1988). As stated by Levi (1992) *Gasteracantha* also has carapace humps but they are much smaller. The abdomen is often tuberculate, is high in the front and overhangs the carapace where it fits snugly into the space behind the caput humps. The epigynum in Australian species is basally broad with a short, pointed or long, finger like scape hinged at the front then directed backwards (see Davies 1988). Levi (1992) redescribed the males

identified by Simon (1896) as of *C. tuberculata* Keyserling and noted that the carapace had only slight swellings in place of the humps of the female. Other features of the male included concave chelicerae associated with a large palpus, a single macroseta on the palpal patella, a tooth on the endite, and a hook on the first coxa. He also gave some details of the palpal organ. Davies (1988) had earlier stated that many "unmatched" males of *Carepalxis* were known and included male features such as the spur ("hook" of Levi) on coxa I and a single spine ("macroseta" of Levi) on the palpal patella in her generic key of Australian orbweaving spiders.

Biogeography and taxonomy of species.—Levi (1992) recognized three species from Central and South America in his review of the American species. There are currently eight species recognized from Australia and two from New Guinea (Roewer 1942; Bonnet 1956; Chrysanthus 1961).

The occurrence of *Carepalxis* in Australia and Central and South America but not in Africa parallels that of the South American *Taczanowskia* Keyserling 1879 and the Australian *Celaenia* Thorell 1868 (the latter also occurs in New Zealand) which are regarded as sister genera (Simon 1895; Eberhard 1981; Levi 1996). Such a geographic disjunction suggests that *Carepalxis* was established as a genus at least by the early Tertiary before the separation of South America and Australia but after the breakaway of Africa post-Jurassic.

All currently recognized Australian species (Bonnet 1956; Roewer 1942; Brignoli 1983) are from eastern Australia. All types are females and their localities and depositions follow. *Carepalxis beelzebub* (Hasselt) 1873, Melbourne Victoria, Amsterdam Netherlands; *C. bilobata* Keyserling 1886, Peak Downs Queensland, Museum Godeffroy now in Zoologisches Institut und Museum (ZMH) Hamburg; *C. coronata* (Rainbow) 1896, New England New South Wales, Australian Museum (AM) Sydney; *C. furcula* Keyserling 1886, Peak Downs, Queensland, ZMH; *C. lichensis* Rainbow 1916, Gordonvale, Queensland, AM; *C. montifera* L. Koch 1872, Mackay, Queensland, ZMH; *C. poweri* Rainbow 1916, Narabeen New South Wales, AM; *C. tuberculata* Keyserling 1886, Sydney New South Wales, Rockhampton and Peak Downs Queensland, ZMH.



Figure 1.—Distribution of *Carepalxis* in Western Australia.

Of the American species, Levi (1992) considered *C. camelus* Simon from Paraguay and Argentina to be the most similar to the type species, *C. montifera* from Queensland, Australia. This opinion appeared to be based on similarity of the long scape of the epigynum of *C. camelus* and illustrations by Davies of a specimen identified by her as *tuberculata*.

Records of *Carepalxis* from Western Australia: *Carepalxis* is now recorded from Western Australia for the first time. There are 44 specimens of the genus in the Western Australian Museum and three in my collection (BYM) held at the Zoology Department, University of Western Australia. These appear to belong to seven species, three of which show similarities to *C. tuberculata*, *C. furcula* and *C. beelzebub*. Locality records are indicated on the map in Fig. 1 showing the scattered, wide distribution in Western Australia from the tropics and arid interior to the mesophytic and coastal southwest.

The apparent central gap in the continental distribution is anomalous. Although there is a tendency to think of Gondwanan distributions as pertaining to southern Australia (and there are many such relictual distributions), clearly some Gondwanan genera occur also in the tropics and even arid regions. Within the Araneidae, *Celaenia* Thorell (sister genus of the South American *Taczanowskia* Keyserling) has a continental distribution, including arid habitats. Considering the wide (although apparently disparate) geographic range of *Carepalxis* on both "sides" of the Australian con-

tinant it would be expected to range also from Darwin to Adelaide through the center.

NATURAL HISTORY OBSERVATIONS AND DISCUSSION

Predation.—Thirty of the 44 specimens of *Carepalxis* in the WAM collection were found in dissected mud wasp nests. Twenty-eight of these, from Sabina River near Busselton, were from eight nests (which also included other Araneids) made by solitary wasps of a *Polis* sp. (J. Waldock pers. comm.). Of the other two specimens, one from Kathleen Valley was reported by the collector to have come from “a hornet’s nest packed with spiders,” the other from Darlington (near Perth) was recorded as “prey of a wasp.” It is well known that various mud-dauber pompilids prey on araneid spiders which they seek out while the spiders are resting during the day. Also of interest and direct relevance is Rainbow’s record of a specimen of *Carepalxis bilobata* Keyserling 1886 “from nest of *Scelephron* sp.” from Cooktown, Queensland (Rainbow 1916). Other predators probably include birds such as honeyeaters which are well known for their habit of searching out spiders as prey.

Mimicry and web.—On 24 May 1980 in West Cape Howe National Park I was surprised to observe a specimen of a *Carepalxis* species sitting among some buds of a jarrah tree (*Eucalyptus marginata* Donn. ex Sm.) (see Main 1988 for description of the site). The spider was unnoticed, until it flexed and retracted its legs. This was due to its striking resemblance to the seed capsules (gumnuts) borne abundantly on the jarrah tree along with developing flower buds. This resemblance resulted from the shape and colour of the spider’s abdomen. The “folium” or leaf pattern on the back of the abdomen was much darker than the general background color. The folium was not posteriorly attenuated as in many araneids such as *Araneus* Clerck 1757 and *Eriophora* Simon 1864 species, but was longitudinally compressed and roughly circular in outline. This, combined with the characteristic squat and dorsally flattened shape of the abdomen, presented in profile an urn shape (like a smooth-walled, woody jarrah “nut”) and dorsally the dark, truncated pseudo-folium resembled the opening of the nut from which the seeds are shed (Figs. 2, 3 & 4).

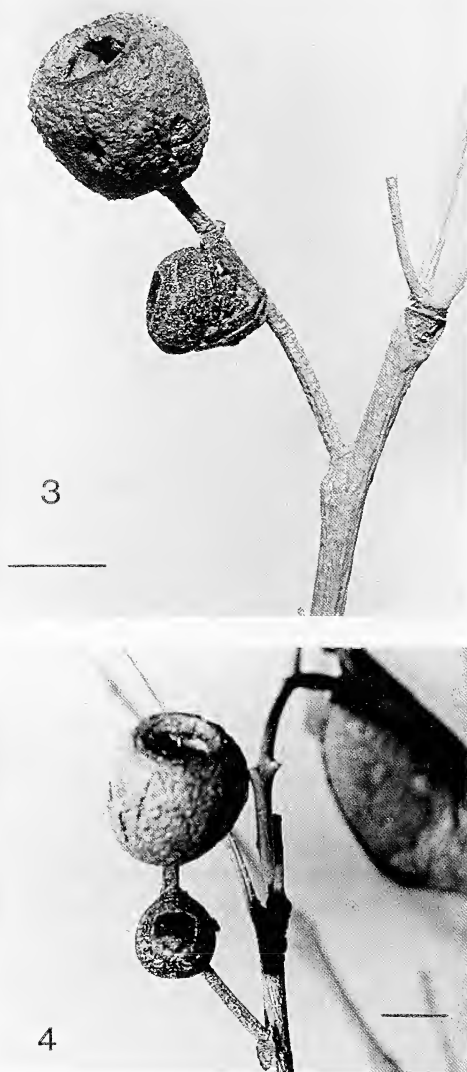
Web construction: The spider was kept



Figure 2.—Jarrah “nut” (seed capsule) and *Carepalxis* mimic, oblique profile view. (Scale bar = 5.0 mm).

alive in the laboratory for a month to observe its behavior. Dry jarrah twigs with gumnuts were stood in a small container of soil and over these was placed a large glass battery jar (18 × 20 × 28cm). The spider constructed a horizontal line between the ends of two terminal twigs and hung suspended from the line each night for 15 nights. The spider appeared to hold the thread with the first legs outstretched in front and with the fourth legs stretched behind. Legs 2 and 3 were bent close to the body but also held the thread. It varied its position at either end of the thread on different nights. The first day after constructing the thread the spider rested on the floor of the cage. Thereafter, when away from the thread it took up a position against a gumnut to which it showed a remarkable resemblance. After 15 days the spider constructed, during one night, a complete vertical orbweb and hung suspended upside down at the hub. The sticky spiral began some distance from the hub which appeared to be “open.” It is remarkable that the spider was able to construct the web in the absence of any appreciable air currents below the battery jar.

There are few references to the web of *Carepalxis*. However, Rainbow (1909) referred to the typical “orbicular” web of *C. tuberculata*. Rainbow (1916) also described (from a collector’s notes) three spherical egg cocoons of



Figures 3, 4.—Jarrah “nut” and *Carepalxis* mimic “perched” on stem below nut. 3. Profile view of spider; 4. Dorsal view (or “rear” view of abdomen) of spider. (Scale bars = 5.0 mm).

Carepalxis lichensis Rainbow 1916, “suspended in a horizontal line in forest tree.”

Mimicry in araneid spiders: Over a century ago Rainbow (1896) in his dissertation on protective coloration and mimicry of spiders cited several examples of mimicry in Australian Araneidae. These included “mimicry” and concealment of egg cocoons. However, most examples were of spiders fitting one of the following three categories. (1) Those which

resembled parts of plants through a combination of color and pattern; such mimicry was interpreted as helping the spiders to avoid attack by birds and reptiles. Rainbow listed the following instances in this category: (a) *Epeira ficta* (= *Araneus fictus* (Rainbow 1896)) and *E. similis* (= *Zealaranea crassa* (Walkenaer 1842)) which “mimics” leaves exhibiting patterns of holes caused by insect attack. (b) *Acrosoma* Perty 1833, which bears a likeness to thorny leaves and “knots” of shrubs. (c) *Tetragnatha* Latreille 1804, *Phonognatha* Simon 1894, and *Epeira higginsii* (L. Koch 1871 (= *Arachnura higginsii* (L. Koch))) (all at that time included in the Argiopidae (= Araneidae)) which have a likeness to twigs and/or leaves. Not mentioned by Rainbow is the notable blend of *Dolophones* Walkenaer 1837 with twigs around which it wraps the broad, flattened abdomen thereby eluding visual detection. (2) Those spiders which bear a likeness to insects that are unpalatable to birds (i.e., Batesian mimicry), e.g., *Cyrtarachne caliginosus* (Rainow 1894) (= *Ordgarius furcatus* O.P. Cambridge 1877)) in which the male has hairs that mimic in appearance the irritating hairs of certain caterpillars. (3) Those spiders which attract insect prey, e.g., *Celaenia excavata* (L. Koch 1867) which through its resemblance to a bird dropping, Rainbow suggested lured potential insect prey in “quest of food.”

“Gumnut” mimicry as protection against predators: There do not seem to be documented examples of araneids with such precise specific plant models as that of the “gumnut” *Carepalxis* recorded here, the advantage of which is assumed to be protection against bird predators. In this light it is of interest that four of the *Carepalxis* specimens in the WAM collections found in dissected wasp nests show a remarkable similarity to the West Cape Howe gumnut mimic. The specimens are not in ideal condition and some are shrivelled but show a distinctly dark, modified folium roughly circular in outline on a lighter ground. In that such wasps are diurnal hunters the spiders must have been searched out while resting rather than when exposed in a web. Hence although the mimicry may protect the spiders from birds such as honeyeaters which are very persistent in their foraging amongst foliage, clearly some wasps are able to detect them.

Development of "gumnut" mimicry.—Many araneid genera, e.g., *Araneus* Clerck 1857 and *Eriophora* Simon 1864 have a leaf-like (folium) pattern on the dorsum of the abdomen. The folium margin is frequently stencilled and the folium itself may be a different color to the background color of the integument. Some species exhibit a distinct polymorphism for color patterns which may be fixed throughout life. For example, *E. biapicata* (L. Koch 1871) shows a range of color combinations through greys and browns of folium and background, with the folium toning or contrasting with the abdomen background color. Some individuals appear to lack pigment in the folium area with the guanin deposits showing through the integument as a white folium patch or arrowhead (see Main 1976, Pl. 36; as *Araneus transmarinus* (Keyserling 1865)).

Spiders rest away from their webs during the day on foliage, seed heads, bark and buildings. Matching colors of spiders and background is often striking. Nevertheless it is doubtful whether these spiders can change color abruptly or at all after the first few instars. It is more likely that selection occurs on spiderlings during their early instars. However, there is certainly scope for manipulation and experimentation with spiderlings on different backgrounds to test colour modification.

Species of *Carepalxis* possibly exhibit color variations amongst individuals like other araneids, particularly *Eriophora*. Thus selection could favor those individuals with a dark abdominal patch (gumnut mimics) which would be less conspicuous to birds (at least for spiders hosted in jarrah foliage). The questions to ask now are: Is there variation in initial color patterns within cocoon clutches? If so, is there selection according to differential foliage settlement, i.e., on jarrah versus other vegetation in relation to color pattern (gumnut versus non-gumnut mimics)?

Observations and museum collections suggest that *Carepalxis* spiders, of any design, although geographically widespread, are rare. Such perceived rarity poses real difficulties for a biologist's analysis of the mimicry. However, the wasps know otherwise!

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EFFECTS OF SHORT-TERM SAMPLING ON ECOLOGICAL CHARACTERIZATION AND EVALUATION OF EPIGEIC SPIDER COMMUNITIES AND THEIR HABITATS FOR SITE ASSESSMENT STUDIES

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ABSTRACT. Epigeic invertebrates such as spiders are of increasing importance for habitat characterization and for assessments within environmental plannings in Germany and other European countries. Due to high costs for spider sampling (e.g., with pitfall traps), proposals for a limited sampling effort are required for the practical use. The results of a two-year study with continuous sampling are compared to results of short-term sampling and to results of a reduced number of traps. The same data set is used for all evaluations. Decreasing sampling effort generally reduced the number of recorded species and led to a biased ecological characterization of the spider communities. Reducing the number of pitfall traps used provided a more representative sample than did reducing the duration of sampling. In general, errors based on reduced sampling were lower for agricultural than for natural habitats. These results offer practical use of spiders for bioindication in future environmental planning.

The number of epigeic arthropod species which are collected in a specific area depends mainly on the sampling effort, such as on the number of traps or on the length of the sampling period (Stein 1965). One reason for this phenomenon is the finding that rare species or species with short activity periods (but also species living in adjacent habitats) are more likely to be caught with increasing sampling intensity. Therefore, sampling by means of pitfall traps is usually carried out during the entire growing season (in Germany: March–October) and is often repeated in subsequent years to obtain data for a reliable analysis of the species composition of the arthropod community. Unfortunately, there are often limited financial resources for these studies and the results are often required within a short period of time. Therefore, there have been several proposals for a limited investigation program concerning pitfall traps, including the recommendations for sampling periods of only six weeks (Duelli *et al.* 1990) or 10 weeks (Finck *et al.* 1992) or the reduction of the sampling period to only one season (spring or summer; Maelfait & Desender 1990). Alternatively, sampling efforts can be reduced by limiting the number of pitfall traps per habitat.

However, there is little knowledge about the effects of a reduced sampling effort on the

quality of the results, and on the conclusions based on these results. This study tests the effects of short term sampling by: (1) comparing data from an eight week trapping period to data from continuous trapping throughout the season (28 weeks; March–October) and (2) analyzing the results obtained by a reduced number of traps. Data are analyzed to examine both the impact of the reduced sampling effort on species numbers and on the ecological characterization of the spider communities of 20 different study sites.

STUDY AREA

This study was conducted in a typical agricultural landscape south of Bonn (North-Rhine-Westphalia, Germany), which is characterized by intensively-used arable land, meadows, orchards and patchily distributed small forests. Semi-natural landscape elements include small river valleys with adjacent wet grassland, small riparian alder forests, river banks and small patches of abandoned formerly wet pastures. A set of 20 different habitats representing the most important habitat types was investigated along two transects across two valleys (transect I near the village of Pech; transect II near the village of Zuellighoven). These transects ranged from semi-natural to agricultural areas.

Table 1.—List of the investigated sites (I = transect I (near the village of Pech), II = transect II (near the village of Zuellighoven), a = additional site).

Code	Transect	Investigation period	Habitat
for1	I	3/90–10/91	beech-oak forest on acid soil with poor herb vegetation
for22	I	3/92–10/93	beech-oak forest on acid soil with poor herb vegetation mixed with <i>Pinus silvestris</i> and <i>Ilex</i> shrubs
for24	a	3/92–10/93	beech-oak forest on acid soil with poor herb vegetation
alf11	II	3/90–10/91	pastured red alder forest with springs
alf14	II	3/90–10/91	red alder forest with natural flood dynamic
rib5	I	3/90–10/91	shady river bank with red alder riparian forest, mixed with <i>Prunus padus</i>
rib13	II	3/90–10/91	river bank with red alder riparian forest partly mixed with <i>Urtica dioica</i> stands
rib26	a	3/92–10/93	muddy river bank with red alder riparian forest
rib27	a	3/92–10/93	top of river bank 26 with mesotrophic grassland <i>Molinio-Arrhenatheretea</i> -community
pla25	a	3/92–10/93	young plantation of <i>Quercus petraea</i> , mixed with blackberry bushes and birch trees on acidic soil
fal18	a	3/90–10/91	mesophilic fallow surrounded by forests, partly covered with blackberry bushes and young trees (aspen)
rib4	I	3/90–10/91	linear red alder riparian forest close to the river bank exposed to the sun with rich tall herb vegetation
wfal2	I	3/90–10/91	wet fallow (<i>Convolvuletalia</i>), smaller parts with <i>Filipendulion</i> - and <i>Magnocaricion</i> -vegetation
wfal17	a	3/90–10/91	wet fallow with sedges, <i>Carex acutiformis</i> -community, <i>Magnocaricion</i>
wpas12	II	3/90–10/91	wet pasture with <i>Juncus effusus</i>
pas7	I	3/90–10/91	intensively managed mesophilic pasture <i>Lolio-Cynosuretum</i>
pas15	II	3/90–10/91	intensively managed mesophilic pasture <i>Lolio-Cynosuretum</i>
pas19	a	3/90–10/91	intensively managed mesophilic pasture <i>Lolio-Cynosuretum</i> with apple trees, surrounded by forests
field10	II	3/90–10/91	extensively managed crop field with rich stands of weeds, <i>Aphano-Matricarietum</i>
field8	I	3/90–10/91	intensively managed crop field with poor or no weeds

Additionally, some samples were collected in adjacent localities with characteristic habitat types not covered within the transects (Table 1; for details see Riecken 1998).

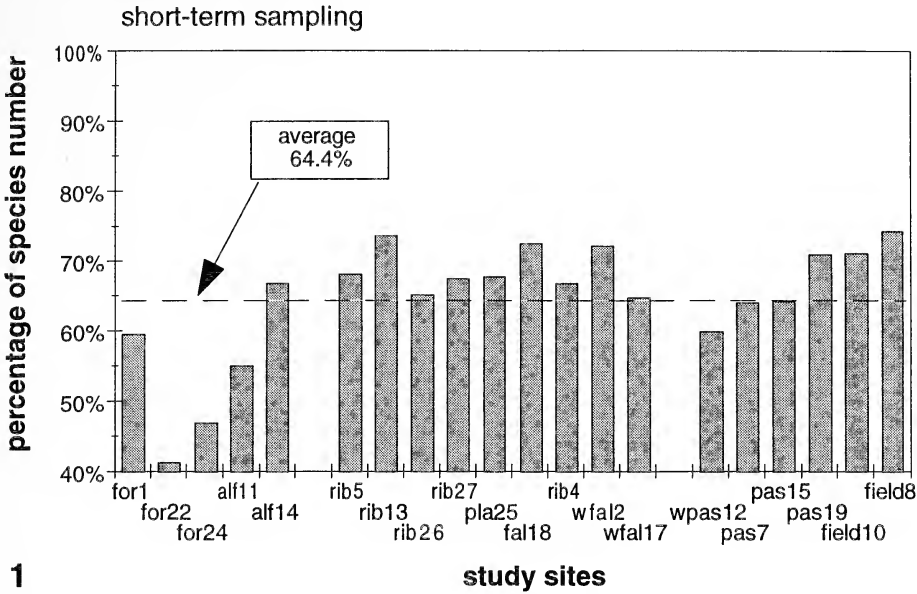
METHODS

Spiders were sampled by means of pitfall traps (350 ml honey-glasses, opening diameter 7 cm), filled with 125 ml of formaldehyde solution (2%) and protected by a roof of a clear acrylic plastic (20 cm × 20 cm). Four traps were exposed at each site (in line, distance 5 m) for two years (for two different periods: 1990, 1991, and 1992, 1993 March to October every year; Table 1). All traps were emptied every two weeks.

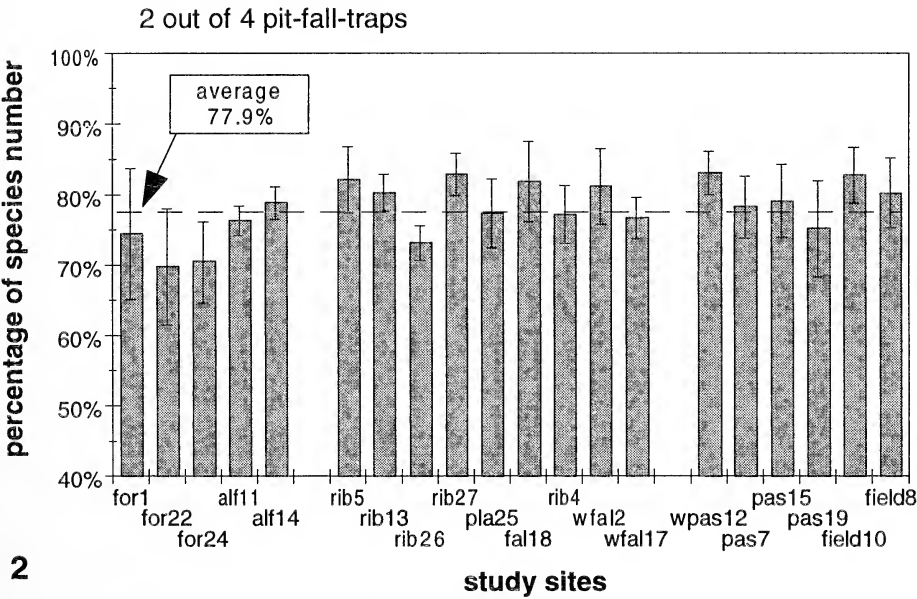
Duelli *et al.* (1990) originally proposed two sampling periods of five weeks a year, with the traps being emptied once a week. Further

analysis should include only data from those three weeks of each period during which the greatest number of specimens were caught. In this study, traps were emptied every two weeks. As it was impossible to take data from three-week periods, two four-week periods seemed to be a good approximation of Duelli's method. Applying this protocol for a limited sampling period resulted in a short-term data set for the following time periods (two four-week periods from both years): sites investigated 1990 and 1991 (see Table 1): 18 May–12 June 1990, 9 August–5 September 1990, 16 May–11 June 1991 and 8 August–5 September 1991; sites investigated 1992 and 1993 (see Table 1): 21 May–16 June 1992, 13 August–9 September 1992, 19 May–15 June 1993 and 12 August–8 September 1993.

Parametric *t*-tests were used for compari-



1



2

Figures 1, 2.—Percentage of species numbers in different sampling protocols. 1. Results from a short-term sampling (eight weeks a year); 2. Results from a reduced data set (average species number from all possible pairs of two out of four pitfall traps) in comparison to the complete data set from sampling throughout two growing seasons (March to October) and all traps.

sons of percentage values (Jongman *et al.* 1987). All data sets were tested for a normal distribution.

All comparisons were made between the results of the complete data set over two seasons

(28 weeks each = 100%) and reduced data sets. I first compared the results from two four-week periods (short-term sampling), and then the results of a reduced number of pitfall traps. In the case of the reduced trap numbers,

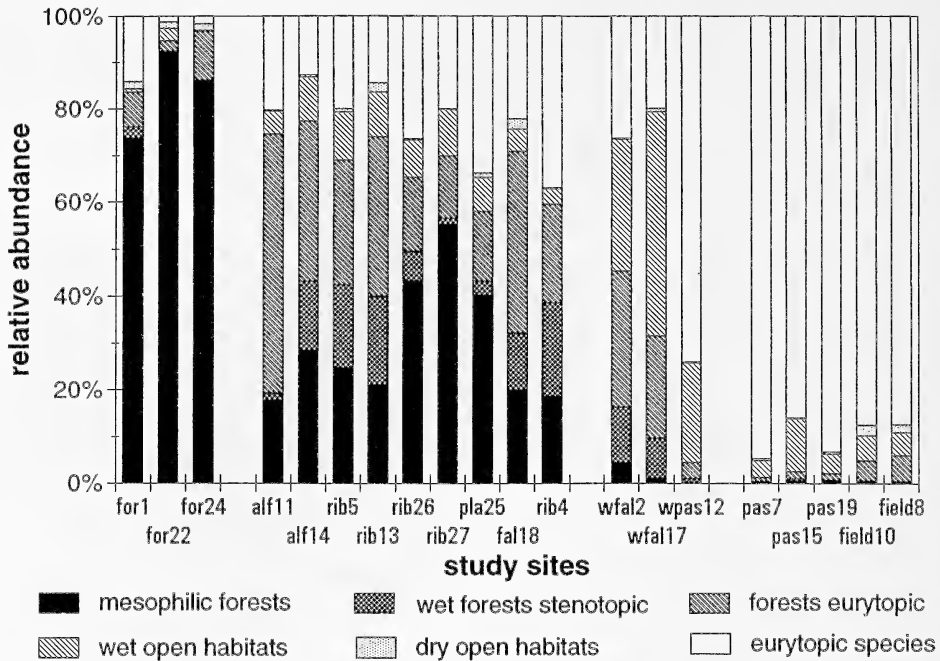


Figure 3.—Composition of the spider communities based on classification of habitat affinity.

the arithmetic means of the results for each trap ($n = 4$) or each possible pair of traps ($n = 6$) were calculated (bars in Figs. 2 and 5).

Habitats were classified by a cluster analysis based on the percentage similarity (Renkonen 1938), using the computer program COMM (Piebenburg & Piatkowski 1992) and the “unweighted pair group method using arithmetic means” (UPGM-linkage). In this method, the distances between clusters are calculated from arithmetic means of the distances between the objects within the compared clusters (Legendre & Legendre 1983).

RESULTS

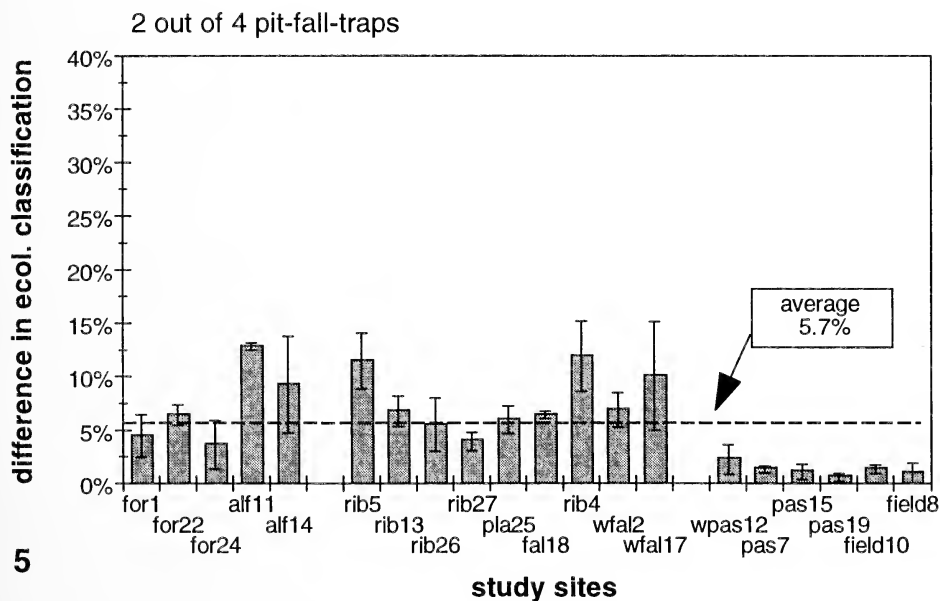
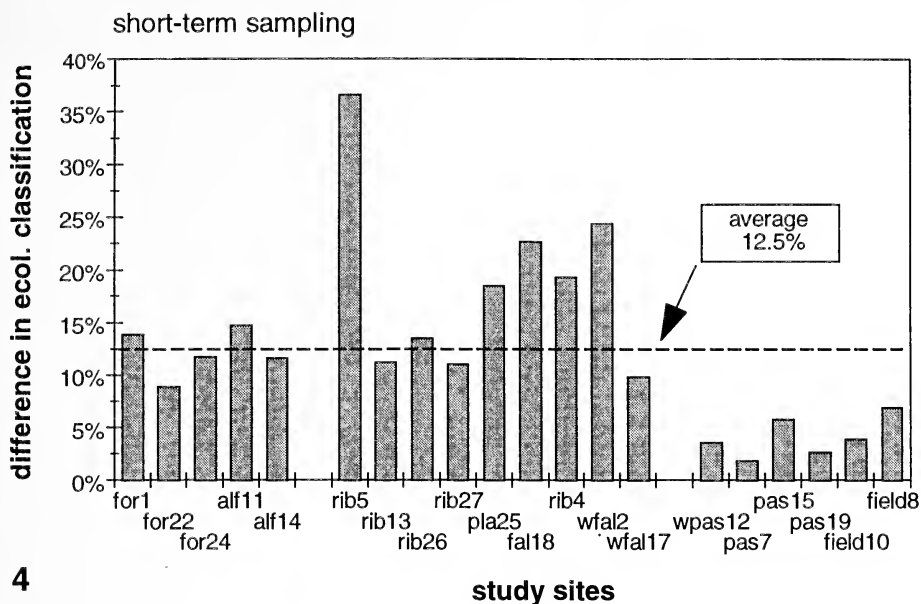
A general analysis, based on a total catch of 50,471 adult spiders belonging to 169 species, showed that Linyphiidae (75.4% of all specimens) and Lycosidae (18.3%) were the most abundant families. Agelenidae (2.3%), Tetragnathidae (1.9%), and Amaurobiidae (1.6%) also occurred regularly. The remaining 17 families comprised only 1.5% of the total catch, but 27% of the recorded species.

Influence of short-term sampling and number of pitfall traps on species numbers.—In the present study, a short-term trapping period as proposed by Duelli *et al.* (1990) would have reduced the number of recorded

species to 64.4% of the initial sample (Fig. 1). In two habitats (forest 22 and 24), less than 50% of all species were included. By contrast, the reduced data set from the intensively used pasture 19 and from the fields contained more than 70% of all species recorded there.

If data from only two of four pitfall traps were used (i.e., a reduction of number instead of time), a significantly higher proportion ($P < 0.001$) of species was included (on average 77.9% of the total number; Fig. 2) in comparison to Duelli’s proposal. Even in the worst case (forest 22 and 24), approximately 70% of all species were included.

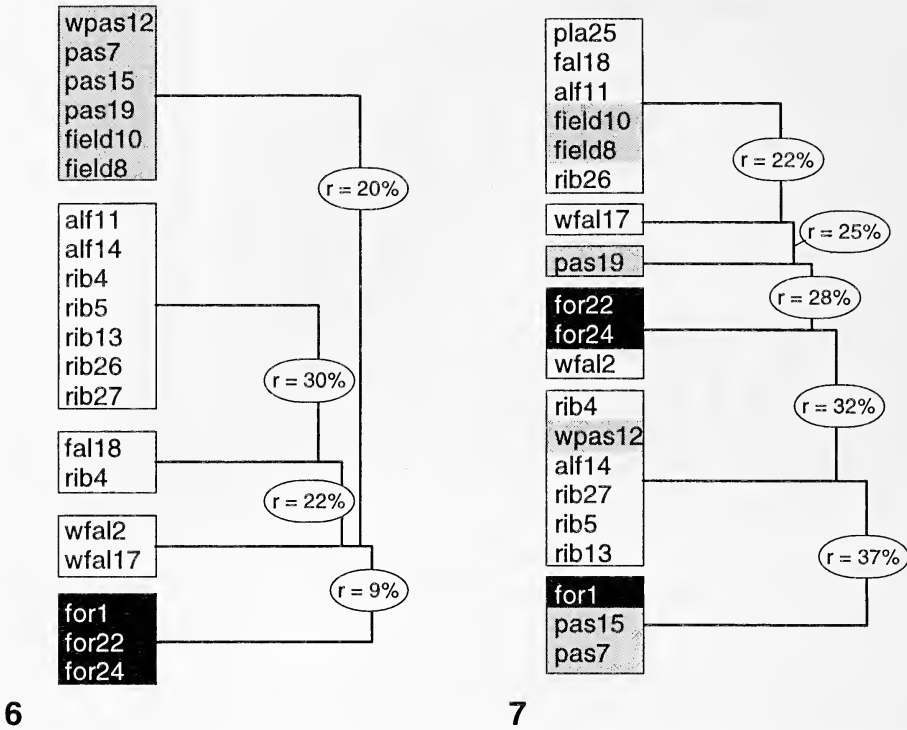
Influence of reduced data sets on the ecological characterization of the spider communities.—Bioindication or planning processes related to nature conservation often require a classification of the habitat preferences or ecological characters of the recorded species. To determine whether a reduced data set would have an impact on ecological characterization of the spider communities, all species were classified based on literature data (Hänggi *et al.* 1995; Platen *et al.* 1991; Reinke & Irmeler 1994; Roberts 1985, 1987, 1995; for further details, see Riecken 1998). The following six habitat affiliations were distin-



Figures 4, 5.—Summarized differences (percentage dissimilarities) in relative abundance of six types of habitat affinity. 4. Affinity resulting from a short-term sampling in comparison to the complete data set from sampling throughout two growing seasons (March–October) and all traps; 5. Affinity resulting from a reduced pitfall number (average of all possible pairs of two out of four pitfall traps).

guished: (1) species restricted to mesophilic forests, (2) species restricted to wet forests, (3) species preferring forests without being restricted to them, (4) species preferring wet open habitats such as bogs, grassland or shores, (5) species preferring dry open habi-

tats, such as meadows or heathers, and (6) eurytopic species that cover a broad range of open habitats, e.g., all types of meadows, fields and fallows. Based on these classification, the community compositions were determined (Fig. 3).



Figures 6, 7.—UPGM-linkage dendrogram based on the “percentage similarity” (RENKONEN-index) classifying the study sites (r = resemblance). 6. Similarities based on the complete data set from sampling throughout two growing seasons; 7. Similarities based on data resulting from short-term sampling.

The dissimilarities (based on the ecological classifications) between short-term data sets and the full data set varied between 1.7% (pasture 7) and 36.6% (river bank 5). The average dissimilarity (pooling all sites) was 12.5% (Fig. 4). When analyzing only 1 out of 4 pitfall traps, the dissimilarities varied between 1.0% (pasture 19) and 20.4% (river bank 4), with an average of 9.6% for all sites. This result did not differ significantly from short-term sampling ($P > 0.05$). Considering data from two pitfall traps (Fig. 5), the results were significantly more similar to the complete data set than the results from short-term sampling were ($P < 0.001$). Here, the dissimilarities varied between 0.6% (pasture 19) and 12.8% (alder forest 11), with an average of 5.6%.

There are two major reasons for the relatively high dissimilarities resulting from a reduced sampling period: the phenology of the dominant species and, depending on it, the differences in phenology of ecological types. Thus, the spider communities are dynamic during the season, both in species composition

and in the relative abundance of ecological types. Therefore, different results can be expected depending on the time frame for sampling, leading to assessment errors and inappropriate nature conservation measures based on bioindication.

In general, errors based on reduced sampling were lower for agricultural habitats (pastures, fields) than for semi-natural sites. The main reason for this finding is the generally low percentage of stenotopic species in all pastures and fields (except the wet pasture 12, see Fig. 3).

Influence of short-term sampling on coenotic comparisons.—The results were also strongly influenced by short-term sampling when different spider coenoses were compared by cluster analysis (UPGM-linkage) based on the “percentage similarity” index (Renkonen 1938). Using the complete data set, five clusters of habitats could be distinguished at a similarity level $> 40\%$ (Fig. 6). This result confirms the expected pattern based on the studied habitat types. For example, all forests and all agricultural sites

were clustered together. The reduced data set, however, produced a completely different result. Even the three quite similar forest sites or the pastures were grouped to different clusters then.

CONCLUSIONS

Short-term sampling reduces the number of recorded species by as much as 50% of the full set. An ecological characterization based on these results is weak, as is a characterization based on a reduced number of pitfall traps, taking only one out of four traps. In contrast to results for carabid beetles (Maelfait & Desender 1990), this reduced data set also leads to important failures in habitat classification and habitat differentiation. Consequently, there will be considerable errors in site assessment. Also, conclusions for planning or for nature conservation activities will be biased if these results are used. Short-term sampling seems to be acceptable only in agricultural habitats. Site assessment studies of epigeic spiders should be carried out throughout the whole growing season (in Germany: March–October). If financial resources are limited, a reduction of the number of pitfall traps will be more appropriate than a reduction of the sampling period.

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DISTRIBUTION AND NATURAL HISTORY OF MEXICAN SPECIES OF *BRACHYPELMA* AND *BRACHYPELMIDES* (THERAPHOSIDAE, THERAPHOSINAE) WITH MORPHOLOGICAL EVIDENCE FOR THEIR SYNONYMY

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ABSTRACT. This comparison of *Brachypelmides* and *Brachypelma* species is based on newly collected spiders and more than 100 specimens from five museum collections. The results show that there are six endemic species of *Brachypelma* in western Mexico (*B. auratum*, *B. baumgarteni*, *B. boehmei*, *B. emilia*, *B. pallidum*, *B. smithi*), presenting a gap in their distribution only where *Brachypelmides klaasi* is found. *Brachypelma vagans* is distributed along both coasts of Mexico and *Brachypelmides ruhnaui* is found in the central part of Mexico. Notes on natural history, a morphological comparison of 27 characters of these genera, and a discussion of the generic affinities are included.

RESUMEN. De junio de 1997 a Octubre de 1998 se hizo un estudio comparativo de *Brachypelmides* y de las especies de *Brachypelma*. Se revisaron especímenes de ambos géneros obtenidos en el campo recientemente y más de 100 especímenes de cinco diferentes colecciones para realizar este estudio. Los resultados muestran que hay seis especies endémicas al Pacífico mexicano de *Brachypelma* (*B. auratum*, *B. baumgarteni*, *B. boehmei*, *B. emilia*, *B. pallidum*, *B. smithi*), presentando una distribución continua a lo largo de la costa del Pacífico, siendo interrumpida por la distribución de *B. klaasi*. *Brachypelma vagans* se distribuye en ambas costas y *Brachypelmides ruhnaui* en el centro del país. Se incluyen notas de historia natural, una comparación morfológica de 27 características de estos géneros y una discusión de las afinidades genéricas.

The subfamily Theraphosinae is a speciose group from the New World, representing some of the most beautiful species of the family Theraphosidae (Pérez-Miles 1992; Schmidt 1993; Smith 1993; Pérez-Miles et al. 1996). The genus *Brachypelma* can be found from Mexico to Costa Rica (Valerio 1980; Smith 1994). The species from the west coast of Mexico are particularly docile and colorful. These traits have led to their being collected in large numbers for the pet trade. The destruction of the natural habitat and the high mortality before sexual maturity (99%) (Baerg 1958) are two factors that affect the populations of these species, and combined with the illegal trade that normally involves the capture of preadult and adult tarantulas, can cause the extinction of these tarantulas. To regulate this trade and prevent their endangerment, all the species of this genus have been listed in appendix II of CITES.

In 1856 White described the first *Brachy-*

pelma species, *B. emilia*, that is endemic to the Pacific coast of Mexico. Since then, another five species have been described that are endemic to this area (*B. auratum*, *B. baumgarteni*, *B. boehmei*, *B. pallidum*, *B. smithi*) (Schmidt 1992; Smith 1993; Schmidt & Klaas 1994; F.O.P. Cambridge 1897). *Brachypelma vagans* Ausserer 1875 inhabits the same area but populations also exist along the Gulf of Mexico down to Costa Rica. *Brachypelma epicureanum* (Chamberlin) 1925 is found only in the Yucatan peninsula (Smith 1994).

Schmidt & Krause (1994) described a new species of Theraphosinae from the west coast of Mexico. Although this tarantula is very similar to those of *Brachypelma*, they argued that it should be placed in a new genus because it has a pad of plumose hairs on the femur IV, the males present a sharp tapered embolus, and the females have a bipartite and wide spermatheca. The species was named *Brachypelmides klaasi*. However, in the same

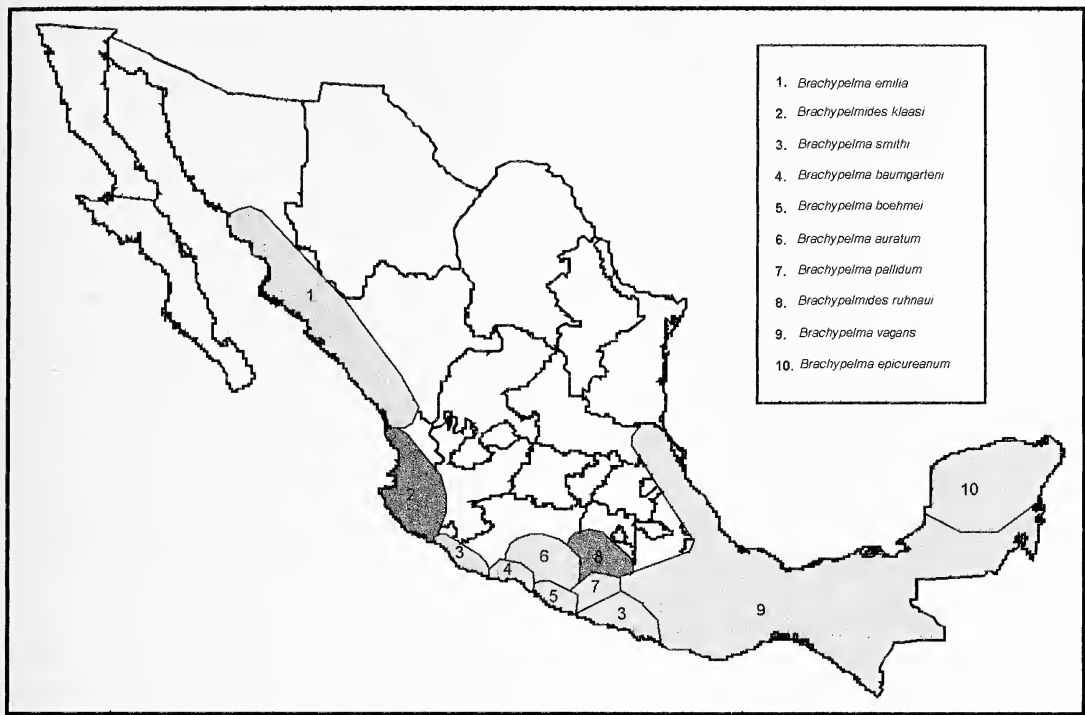


Figure 1.—Distribution of the species of *Brachypelma* and *Brachypelmides* in Mexico.

year Smith (1994), after examining the types, concluded that *B. klaasi* belongs to the *Brachypelma* group, being only “its most extreme form.” Pérez-Miles et al. (1996) made a systematic revision and a cladistic analysis of Theraphosinae, but they did not include *Brachypelmides* in their analysis. Schmidt (1997) described another new *Brachypelmides* species from the central region of Mexico, *B. ruhnaui*, adding support to his idea that *Brachypelmides* is a valid genus.

Our research of the species of *Brachypelma* and *Brachypelmides* brings more data to the question of the distinctness of these genera. It also adds information on the natural history and distribution data for these tarantulas.

METHODS

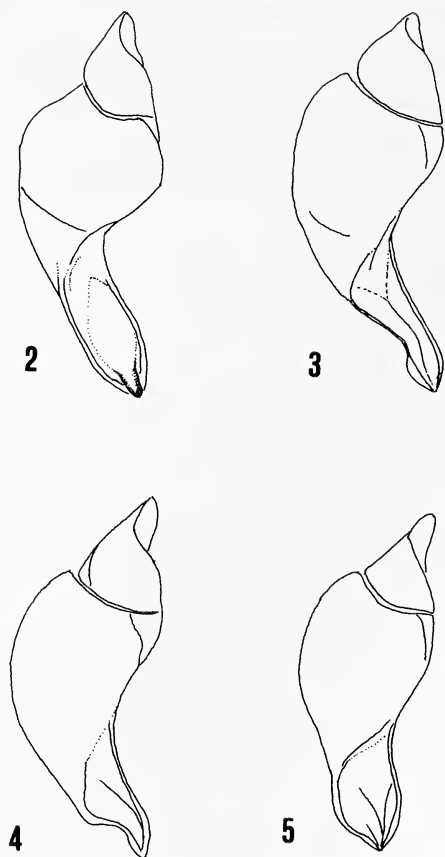
The collections visited and used for the study included the following: the American Museum of National History, the California Academy of Sciences, Field Museum, Instituto de Biología, UNAM, in Mexico City (IBUNAM), and Estación de Biología, Chamela, in Jalisco. The five collections have together more than 100 specimens of both gen-

era. All collection data were recorded. No types were studied.

Fifteen field trips were made to the west coast of Mexico from June 1997 to October 1998, and two more to the east coast in this same period. Ecological and geographical data were taken, and the specimens were brought to the lab in Mexico City Laboratorio de Acarología “Anita Hoffmann.” Live specimens were put in controlled environment chambers where their reproductive behavior was studied (Yáñez & Loch 1998). The morphological characteristics of preserved specimens were analyzed in more detail, and the figures presented in this work were made from them. The specific collecting data for specimens are not given, but a range map (Fig. 1) is included because we wish to protect the species from the illegal pet trade.

DISTRIBUTION

Brachypelma is a common genus in the Pacific and Gulf coasts of México; the distribution of species along the west coast is only interrupted by that of *Brachypelmides klaasi*, and in the central part by *B. ruhnaui* (Fig. 1).



Figures 2–5.—Frontal view of the right bulbs of four species of tarantulas. 2. *Brachypelma vagans* right bulb; 3. *Brachypelmides ruhnaui* right bulb; 4. *Brachypelmides klaasi* right bulb; 5. *Brachypelma smithi* right bulb.

Brachypelma smithi has a disjunct distribution, and *B. vagans* has the largest distribution. The only distribution that we could not verify was that for *B. epicureanum*, which is endemic to the Yucatan peninsula (Smith 1994). Field and collection data corresponded in all other species. The distributions given by Smith (1994) did not correspond with ours in all cases, but they are generally not contradictory. The other collecting data found in the descriptions of the species coincide with the areas shown in Fig. 1 (White 1856; Ausserer 1875, F.O.P. -Cambridge 1897; Schmidt 1992; Schmidt 1993; Smith 1993; Schmidt & Klaas 1994; Schmidt 1997; Loch et al. 1998).

NATURAL HISTORY

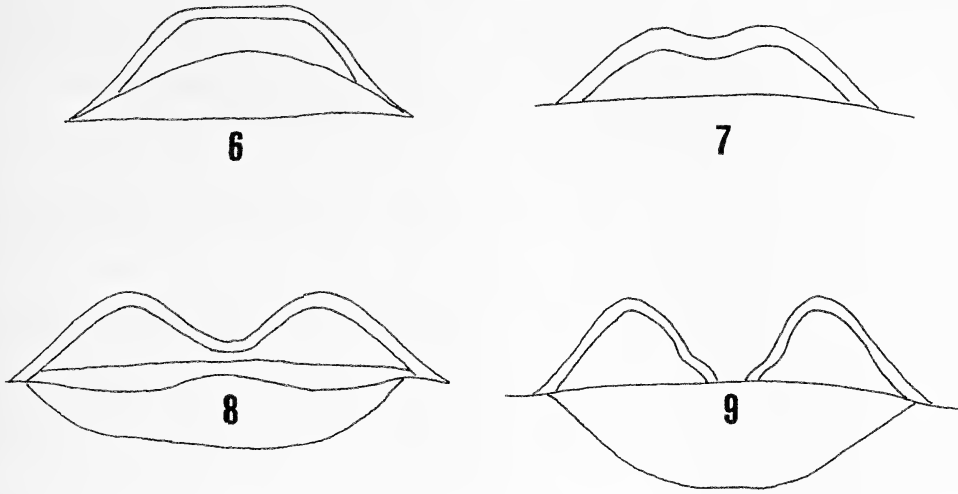
The natural history of *Brachypelma* species differs little if at all from the *Brachypelmides*

species. The following data are field and laboratory observations of the two genera.

Burrow Construction.—All the species studied live in burrows found in the soil, sometimes near rocks or trees, sometimes in open field, but not far from vegetation. They have only one entrance, a little wider than the tarantula's body size. When the tarantula is active this entrance is clean and some silk can be found. When the tarantula is inactive for a long period the entrance is covered by soil and leaves that the tarantula gathers with silk. A horizontal tunnel leading from the entrance is normally three times larger than the tarantula. This tunnel is followed by a chamber 2–3 times bigger than the tarantula, where it molts, then a vertical tunnel shorter than the first one that ends with a larger chamber, where the tarantula rests and eats its prey. The mature female's burrow in the reproductive season has more silk in the entrance than usual.

Phenology.—The tarantulas of these genera are long-lived. The males can reach maturity in 7–8 years, living only one year or less after the last molt, while the females reach maturity in 9–10 years, then live 10 more years. Compared to other genera of the same subfamily, they grow slowly (Smith 1994). In all species pre-adults and adults molt at the end of the dry season (June–November), males begin to wander in search of the females after they molt, and the females lay an egg-sac before they molt. The egg-sac hatches 3–4 weeks before the rainy season begins. Males of all west coast species wander during daylight, particularly in the morning and in the evening, while the species of the east coast and center wander at night.

Color pattern.—*Brachypelma klaasi* coloration is very similar to that of the six species of *Brachypelma* that are endemic to the west coast. *Brachypelma boehmei* is the more similar, having, like *B. klaasi*, black tarsi, orange-yellow metatarsi, tibiae and patellas, black femora and coxae and orange-yellow hairs on the opisthosoma. It differs only in the carapace, which is yellow-orange in *B. boehmei* and black in *B. klaasi*. *Brachypelma baumgarteni* is also very similar, but it has a more reddish patella. *Brachypelmides ruhnaui* has the same coloration of *B. vagans* and *B. epicureanum*, differing only in having a yellow carapace, rather than black as in the others. Although all the species have striking col-



Figures 6–9.—Dorsal view of the cleared spermathecae of four species of tarantulas. 6. *Brachypelma auratum*; 7. *Brachypelma emilia*; 8. *Brachypelma vagans*; 9. *Brachypelmides klaasi*.

oration, they are in fact cryptic within their native habitat, making it very difficult to see the tarantulas, even when they are out of their burrows in daylight.

DISCUSSION OF GENERIC AFFINITIES

The data on distribution and natural history provide support for the hypothesis that these species are closely related. In the cladistic analysis of Pérez-Miles et al. (1996) 27 characters were used. The characters in *Brachypelma* are: palpal bulb with concave/convex apical region; relative width of sclerites II + III (measured at 20% of its length, from the apex) wide (equal to or more than 10% of the length of the bulb); lack of the paraembolic and digitiform apophysis; presence of smooth peripheric and supernumerary keels; and a large subtegulum. The male's tibia lacks a lateral process in the retrolateral region, a retrolateral cluster of spines and a prolateral process. It has two tibial apophyses; metatarsus I lacks a basal process and is not strongly curved, its flexion provided by the outer side of the tibial spurs. Spermatheca widely fused and with unilobulated receptacles; femur III and tibia IV not incrassate; femur IV without a retrolateral scopula; urticating hairs type I and III present, type IV are absent. Trochanteral and coxal stridulatory hairs absent; coxal spinules are absent; numerous labial cusps present; fovea without a spherical process.

We compared all 27 characters among the 10 species analyzed and found that *Brachy-*

pelmides has only one character that distinguishes it from *Brachypelma*. This character is the presence of a spermatheca with two receptacles separated or only partly fused. However, in the genus *Brachypelma* some spermathecae are widely fused (*B. smithi*, *B. auratum*), some semi-divided (*B. emilia*, *B. baumgarteni*, *B. boehmei*) and some only partly fused (*B. vagans*) (Figs. 6–9).

The palpal bulb morphology, principally in the embolus, is distinctive in all the species. *Brachypelmides klaasi* and *B. runhau* have the embolus sharper and more tapered, but do not differ in the characteristics above listed from *Brachypelma*. The palpal bulb of *B. klaasi*, being wider, is more similar to that of *Brachypelma* species from the Pacific coast. The bulb of *B. ruhnaui* bulb is more similar to the thinner bulb of *B. vagans* (Figs. 2–5).

The diagnosis of *Brachypelma* (Pérez-Miles et al. 1996) shows that this genus does not have retrolateral scopulae on femur IV. We examined the two species of *Brachypelmides*, and we found no scopulae on the retrolateral face of the femur IV. We found plumose hairs in both genera. The patch of plumose hairs mentioned for *B. klaasi* as a new character separating these genera is not mentioned in *B. ruhnaui* (Schmidt & Krause 1994; Schmidt 1997); and we could not find it in this species, so this would only be a characteristic that distinguishes *B. klaasi*. Another characteristic that *Brachypelmides klaasi* shares with the

species of *Brachypelma* is that it is very popular in the pet trade, but *Brachypelmides* is not listed in appendix II of CITES.

Although, the distribution and morphology likely provide strong evidence that *Brachypelmides* and *Brachypelma* are one and the same genus, a revision of all the species of these genera, not just those from Mexico, using cladistic analysis will provide a strong basis for placing the two species of *Brachypelmides* in the genus *Brachypelma*.

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COMMON GROUND-LIVING SPIDERS
IN OLD TAIGA FORESTS OF FINLAND

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ABSTRACT. Spiders living on the forest floor in six old taiga forests were studied using pitfall traps in 1994 (in Suomussalmi) and 1995 (in Puolanka), central-eastern Finland, ca. 65° N. Seventy-seven species belonging to eleven families were caught. Linyphiidae (s. lat.) dominated both in species and individual numbers. The most common species were *Lepthyphantes alacris*, *Agynera ramosa*, *Lepthyphantes antroniensis*, *Centromerus arcanus* and *Agynera subtilis*. The fauna found is, in general, typical of old Finnish boreal forests.

The spider fauna of the boreal (taiga) forests in Finland has been studied by many authors. Basic studies were carried out by Huhta (1965, 1971). Investigations on spiders in old, primeval forests of Finland include, e.g., pa-

pers by Palmgren & Biström (1979), Biström & Väisänen (1988), Väisänen & Biström (1990), Niemelä et al. (1994) and Pajunen et al. (1995). These are all from more southern areas of Finland.

The spiders of taiga forests in central-eastern Finland have not been studied. The aim of this brief paper is to present the abundant species (of the early-midsummer period) on the floor in six old taiga forests. Some comparisons with previous studies will also be made.

These old forests are in the interests of the pulp and paper industry, and, on the other hand, there are plans to protect these areas. This study was supported by the Kainuu Park Area of the Finnish Forest and Park Service in order to provide some basic data for planning the use of these old forests. The data from the research in Suomussalmi have been partly published (Koponen 1995).

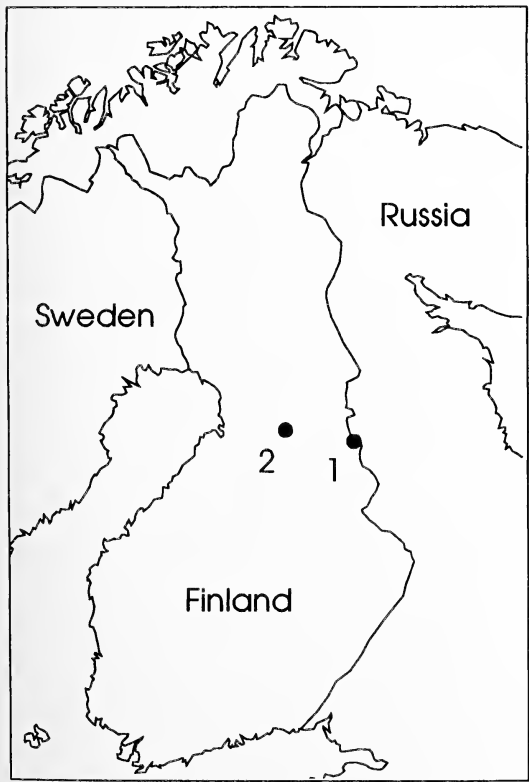


Figure 1.—The study areas in central-eastern Finland. 1, Suomussalmi; 2, Puolanka.

Table 1.—Percentage of Linyphiidae (s.lat.) of all specimens (A) and of all species caught (B).

Site	A	B
Suomussalmi:		
Luolakangas	95.1	85.0
Likoaho	93.3	72.9
Heinävaara	87.3	71.2
Puolanka:		
Paljakka	97.4	90.5
Kuiriavaara	95.3	73.1
Siikavaara	84.1	74.2

Table 2.—Percentage of the ten most abundant species at Suomussalmi sites, 1994.

Site		Percent
Luolakangas	<i>Lepthyphantes alacris</i> (Blackwall 1853)	22.4
	<i>L. antroniensis</i> Schenkel 1933	21.7
	<i>Centromerus arcanus</i> (O.P.-Cambridge 1873)	11.1
	<i>Diplocentria bidentata</i> (Emerton 1882)	7.5
	<i>Agyneta ramosa</i> Jackson 1912	5.3
	<i>Lepthyphantes tenebricola</i> (Wider 1834)	4.6
	<i>Latithorax latus</i> (Holm 1939)	3.1
	<i>Hilaira herniosa</i> (Thorell 1875)	2.7
	<i>Agyneta subtilis</i> (O.P.-Cambridge 1863)	2.6
Likoaho	<i>Robertus lividus</i> (Blackwall 1836)	2.4
	<i>Agyneta subtilis</i> (O.P.-Cambridge 1863)	18.7
	<i>Lepthyphantes antroniensis</i> Schenkel 1933	18.7
	<i>Agyneta conigera</i> (O.P.-Cambridge 1863)	7.9
	<i>A. ramosa</i> Jackson 1912	7.6
	<i>Lepthyphantes alacris</i> (Blackwall 1853)	6.5
	<i>Centromerus arcanus</i> (O.P.-Cambridge 1873)	6.1
	<i>Robertus lividus</i> (Blackwall 1836)	5.4
	<i>Lepthyphantes tenebricola</i> (Wider 1834)	5.0
Heinävaara	<i>Alopecosa pinetorum</i> (Thorell 1856)	1.6
	<i>Walckenaeria dysderoides</i> (Wider 1834)	1.5
	<i>Agyneta ramosa</i> Jackson 1912	20.8
	<i>Lepthyphantes antroniensis</i> Schenkel 1933	13.8
	<i>Agyneta subtilis</i> (O.P.-Cambridge 1863)	11.2
	<i>A. conigera</i> (O.P.-Cambridge 1863)	10.3
	<i>Lepthyphantes alacris</i> (Blackwall 1853)	9.9
	<i>Centromerus arcanus</i> (O.P.-Cambridge 1873)	7.4
	<i>Lepthyphantes tenebricola</i> (Wider 1834)	5.5
	<i>Robertus lividus</i> (Blackwall 1836)	4.7
	<i>Diplocentria bidentata</i> (Emerton 1882)	3.6
	<i>Hilaira herniosa</i> (Thorell 1875)	1.2

STUDY AREA AND METHODS

The study areas are old, more or less natural primeval forests, surrounded by cutting areas and by young planted tree formations. The majority of large pines (*Pinus sylvestris*) and spruces (*Picea abies*) have a diameter of 35–45 cm. Dead standing and ground-lying trees are not very common. Field layer is mainly dominated by *Vaccinium vitis-idaea* and *V. myrtillus*, and the ground layer by the mosses of genera *Pleurozium*, *Dicranum* and *Hylocomium*. Elevation of the study sites varies between 160 and 270 m.

There were three study forests situating in the northern boreal forest zone (northern taiga) in Suomussalmi (1994) and three in Puolanka (1995), as follows (Fig. 1): *Suomussalmi* (64°45'N, 29°40'E): - Luolakangas: spruce-dominated, mosaic type (diversified) forest; - Likoaho: relatively dry, pine-domi-

nated forest; - Heinävaara: pine-dominated, more moist than the two previous sites; *Puolanka* (65°N, 28°E): - Paljakka: spruce-dominated forest; - Kuirivaara: spruce-dominated, more moist than the two other sites in Puolanka; - Siikavaara: dry, pine-dominated mixed forest.

Pitfall trapping periods were 13 June–21 July 1994 in Suomussalmi and 14 June–2 August 1995 in Puolanka. The traps were plastic cups (mouth diameter 65 mm). Ethylene glycol with detergent was used as the preservation liquid, and the traps were provided with covers against rain and litter. Altogether, about 5600 identifiable spider specimens were collected. The material has been deposited in the Zoological Museum, University of Turku.

The usefulness of pitfall technique in spider studies has been discussed by many authors (e.g., Lowrie 1985). As pitfall data are not in-

Table 3.—Percentage of the ten most abundant species at Puolanka sites, 1995.

Site		Percent
Paljakka	<i>Lepthyphantes alacris</i> (Blackwall 1853)	33.1
	<i>Centromerus arcanus</i> (O.P.-Cambridge 1873)	22.3
	<i>Agyneta subtilis</i> (O.P.-Cambridge 1863)	7.8
	<i>Macrargus rufus</i> (Wider 1834)	7.4
	<i>Agyneta ramosa</i> Jackson 1912	5.6
	<i>Lepthyphantes antroniensis</i> Schenkel 1933	5.2
	<i>Diplocentria bidentata</i> (Emerton 1882)	3.4
	<i>Hilaira herniosa</i> (Thorell 1875)	3.0
	<i>Cryphoea silvicola</i> (C.L. Koch 1834)	2.2
	<i>Walckenaeria nudipalpis</i> (Westring 1851)	1.9
Kuirivaara	<i>Lepthyphantes alacris</i> (Blackwall 1853)	44.1
	<i>Centromerus arcanus</i> (O.P.-Cambridge 1873)	19.3
	<i>Agyneta subtilis</i> (O.P.-Cambridge 1863)	5.0
	<i>Macrargus rufus</i> (Wider 1834)	4.0
	<i>Agyneta ramosa</i> Jackson 1912	3.7
	<i>Asthenargus paganus</i> (Simon 1884)	3.1
	<i>Lepthyphantes antroniensis</i> Schenkel 1933	3.0
	<i>L. tenebricola</i> (Wider 1834)	3.0
	<i>Pardosa lugubris</i> (Walckenaer 1802)	1.9
	<i>Walckenaeria nudipalpis</i> (Westring 1851)	1.6
Siikavaara	<i>Lepthyphantes alacris</i> (Blackwall 1853)	24.5
	<i>Agyneta subtilis</i> (O.P.-Cambridge 1863)	15.3
	<i>A. ramosa</i> Jackson 1912	13.8
	<i>Zornella cultrigera</i> (L. Koch 1879)	10.7
	<i>Pardosa lugubris</i> (Walckenaer 1802)	10.4
	<i>Centromerus arcanus</i> (O.P.-Cambridge 1873)	9.2
	<i>Walckenaeria nudipalpis</i> (Westring 1851)	4.0
	<i>Lepthyphantes tenebricola</i> (Wider 1834)	2.0
	<i>Agyneta cauta</i> (O.P.-Cambridge 1902)	1.7
	<i>Lepthyphantes antroniensis</i> Schenkel 1933	1.4

dicating real population densities, percentages (not individual numbers) are used here when comparing the sites.

RESULTS

Altogether 77 species were collected. Linyphiidae (s. lat.) clearly dominated in terms of both species and individual numbers (Table 1). This is typical of old, closed and shady forests. Other marked families were Lycosidae, Theridiidae and Gnaphosidae.

The ten most abundant species at each site are shown in Tables 2 and 3. These lists include 14 and 15 species at Suomussalmi and Puolanka sites, respectively. The dominant species in all forests in Puolanka was *Lepthyphantes alacris*, in Suomussalmi the dominants included *L. alacris*, *L. antroniensis*, *Agyneta ramosa* and *A. subtilis*. Non-linyphiids among the abundant species were *Par-*

dosa lugubris, *Robertus lividus*, *Alopecosa pinetorum* and *Cryphoea silvicola*.

In Suomussalmi, three *Lepthyphantes* (*L. antroniensis*, *L. alacris*, *L. tenebricola*) and three *Agyneta* (*A. ramosa*, *A. subtilis*, *A. conigera*) species accounted for 65% of the total material. In Puolanka, *Lepthyphantes alacris*, *Centromerus arcanus*, *Agyneta subtilis* and *A. ramosa* formed 68% of the total material.

Only 14 of the 77 species caught were found in all studied six forests (Table 4). The most common (and evenly occurring) of these linyphiid species were *Lepthyphantes alacris*, *Agyneta ramosa*, *Lepthyphantes antroniensis*, *Centromerus arcanus* and *Agyneta subtilis*. Also the following species were found at all sites but in smaller numbers: *Macrargus rufus*, *Walckenaeria nudipalpis*, *Diplocentria bidentata*, *Tapinocyba pallens* (O.P.-Cambridge 1872), *Lepthyphantes tenebricola*, *Porrhom-*

Table 4.—Species found at all six forest sites; average rank = mean of species' abundance rank (e.g., *Lepthyphantes alacris*: 1st, 5th, 5th, 1st, 1st, 1st = 2.3).

Species	Average rank
<i>Lepthyphantes alacris</i>	2.3
<i>Agyneta ramosa</i>	3.8
<i>Lepthyphantes antroniensis</i>	4.0
<i>Centromerus arcanus</i>	4.2
<i>Agyneta subtilis</i>	5.5
<i>Macrargus rufus</i>	approx. 12
<i>Walckenaeria nudipalpis</i>	13
<i>Diplocentria bidentata</i>	15
<i>Tapinocyba pallens</i>	16
<i>Lepthyphantes tenebricosa</i>	18
<i>Porrhomma pallidum</i>	20
<i>Zornella cultrigera</i>	22
<i>Walckenaeria cuspidata</i>	23
<i>Hilaira herniosa</i>	25

ma pallidum Jackson 1913, *Zornella cultrigera*, *Walckenaeria cuspidata* Blackwall 1833 and *Hilaira herniosa*.

DISCUSSION

The fauna found is relatively typical of Finnish boreal coniferous forests, i.e., taiga. Many of the abundant species have also been observed in old forests in previous studies in southern and central Finland. The northern location (ca. 65°N) of the study areas resulted in the occurrence of several northern species, along with the absence of some species with a more southern range. Väisänen & Biström (1990) listed the eight most abundant spiders found (however, collected with dry funnels) at Saarijärvi (62°50'N; about 300 km SW of the present study area) in central Finland. Of these eight species, only *Centromerus arcanus* was both abundant and common, six other species were found in smaller numbers and one was absent in the present material.

Some of the present abundant species have northern general range in Finland being rare or absent in earlier studies on old forest spiders carried out in more southern areas of southern or central Finland (e.g., Palmgren &

Biström 1979; Biström & Väisänen 1988; Väisänen & Biström 1990; Niemelä et al. 1994; Pajunen et al. 1995). These include, e.g., *Lepthyphantes antroniensis*, *Latithorax latus*, *Zornella cultrigera* and *Hilaira herniosa*.

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ABUNDANCE AND PHENOLOGY OF SCHIZOMIDA (ARACHNIDA) FROM A PRIMARY UPLAND FOREST IN CENTRAL AMAZONIA

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ABSTRACT. There were 193 schizomids (hubbardids) collected from the soil (0–7 cm depth) during a 12 month study of a primary upland forest (37.5 ± 16.8 ind/m²/month) near Manaus. They were represented by *Surazomus brasiliensis* (Kraus 1967) and an undescribed species of a new genus (96% and 4% of the total catch, respectively). About 68% of all specimens of *S. brasiliensis* inhabited the organic soil layer (0–3.5 cm depth) where monthly catches of juveniles were positively correlated with soil temperature. Females were twice as abundant as males. The lack of a distinct reproductive period and the presence of juveniles (in particular the first nymphal instar) and adults (both sexes) throughout the year indicate a plurivoltine mode of life. Few specimens were caught on the soil surface, and none were on tree trunks or in the canopy. Abundance of *S. brasiliensis* is compared to that of the Palpigradi (micro-whip scorpions) and Thelyphonida (vinegaroons) from the same study site.

The order Schizomida is comprised by about 180 described species. Few studies have been conducted on their ecology and biology. Schizomids are considered to be hygrophilous, photophobic, hemiedaphic inhabitants of soils, particularly in the tropics and subtropics. Some species are termitophiles, myrmecophiles, nidicoles or troglobites. (cf. Moritz 1993; Humphreys *et al.* 1989; Reddell & Cokendolpher 1995; Rowland 1972).

In Central Amazonian forests, schizomids represent less than 1% of the soil arthropods which mostly inhabit the top 7 cm (cf. Adis *et al.* 1987, 1989). Our material, obtained in a primary upland forest over a 12 month period, represents the very first contribution on the abundance and phenology of a Neotropical schizomid species: *Surazomus brasiliensis* (Kraus, in Kraus & Beck 1967).

STUDY AREA AND METHODS

Schizomids were collected between 1981–1983 in the course of ecological studies on Central Amazonian arthropods from a previously investigated and fully-described primary upland forest at Reserva Florestal A. Ducke (= Reserva Ducke; 2°55'S, 59°59'W; Penny & Arias 1982). The reserve is located on the

Manaus-Itacoatiara highway (AM-010), about 26 km from Manaus. The forest is subject to a rainy season (December–May; average precipitation 1550 mm; 258.9 ± 36.8 mm/month) and a “dry” season (June–November: average precipitation 550 mm; 91.8 ± 43.8 mm/month and each month with some rain events; Ribeiro & Adis 1984). The yellow latosol (= ferrasol in Jordan 1984) of the primary upland forest had a 2–3 cm thick humus layer, interspersed with fine roots, and a thin surface covering of leaf-litter.

One ground photo-eclector (emergence trap) and one arboreal photo-eclector for trunk ascents (funnel trap) were installed in the forest (cf. Adis & Schubart 1984) and remained there from December 1981 to December 1982. Distribution of schizomids in the soil was studied between September 1982 and August 1983 (Moraes 1985). Twelve soil samples were taken once a month every 2 m along a randomly selected transect. The split corer, composed of a steel cylinder with lateral hinges (diameter 21 cm, length 33 cm), was driven into the soil by a mallet. Each sample of 7 cm depth was then divided into two subsamples of 3.5 cm each for extraction of animals, following a modified Kempson method (Adis

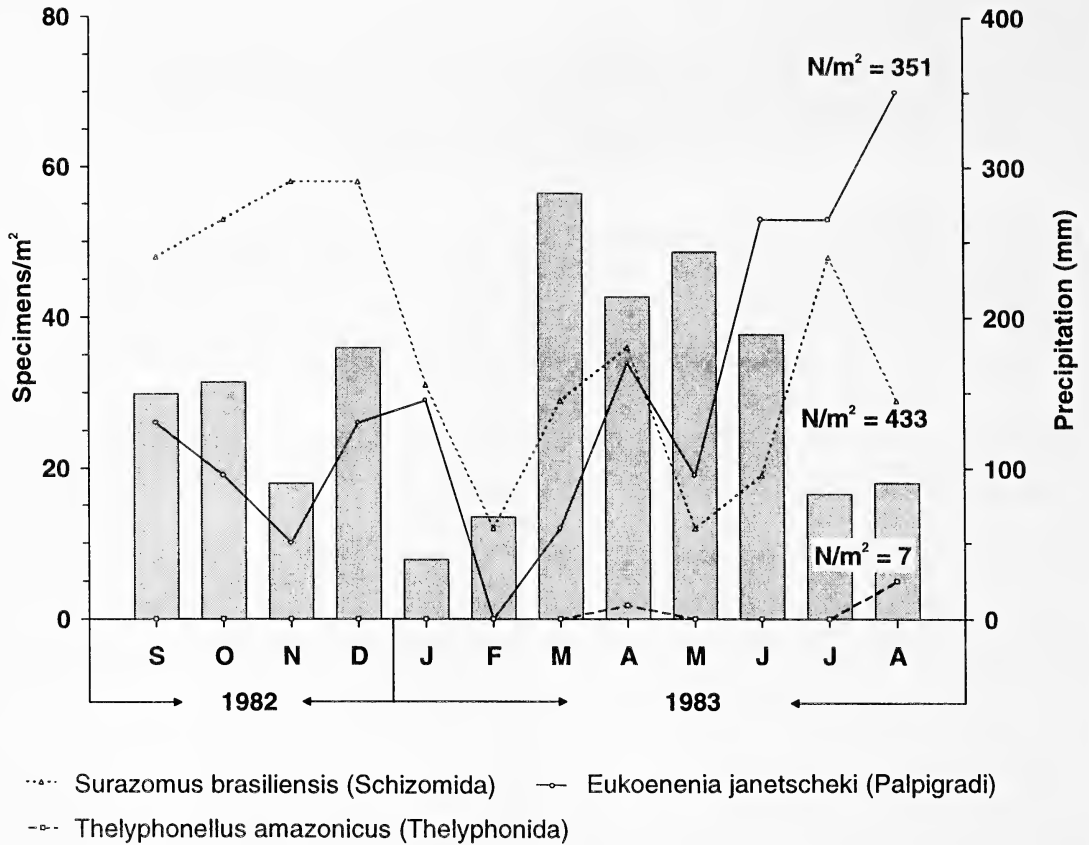


Figure 1.—Distribution of *S. brasiliensis* (Kraus 1967) (Schizomida), *E. janetscheki* Condé 1993 (Palpigradi) and *T. amazonicus* (Butler 1872) (Thelyphonida) in the soil. Samples taken monthly at 0–7 cm depth between September 1982–August 1983 in a primary upland forest near Manaus. (N = total number of specimens). Total precipitation per month given between sampling dates (= at the end of each month). The low rainfall observed in early 1983 was due to a strong El Niño-event (cf. Adis & Latif 1996).

1987). The combined area of the 12 samples represented 0.42 m². Calculated average abundances per m² are given with sample standard deviation. The monthly collection data of schizomids from the two soil layers in relation to changing abiotic conditions (precipitation, temperature and humidity of the air near the forest floor; moisture content, temperature and pH of the soil) were statistically evaluated with a linear, parametric correlation test (Cavalli-Sforza 1972) using the original field data (Morais 1985). In addition, the presence of schizomids in tree crowns of the primary upland forest was tested by fogging canopies with pyrethrum during the dry and rainy seasons (August 1991–July 1994; cf. Adis *et al.* 1997a).
All Schizomida sampled were classified as juveniles, subadults and adults (males and fe-

males, respectively; cf. Reddell & Cokendolpher 1995). Juveniles were tentatively assigned to three size classes, based on the length of the cephalothorax. The size classes presumably represent the three development stages in nymphs, apart from the subadult stage (cf. Brach 1976; Dumitrescu 1973; Rowland 1972).
Voucher specimens have been deposited at the Systematic Entomology Collections of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Brazil, at the Texas Memorial Museum, Austin, Texas and at the Muséum d'histoire naturelle in Genève, Switzerland.
RESULTS
Schizomida obtained from the primary upland forest at Reserva Ducke were represented

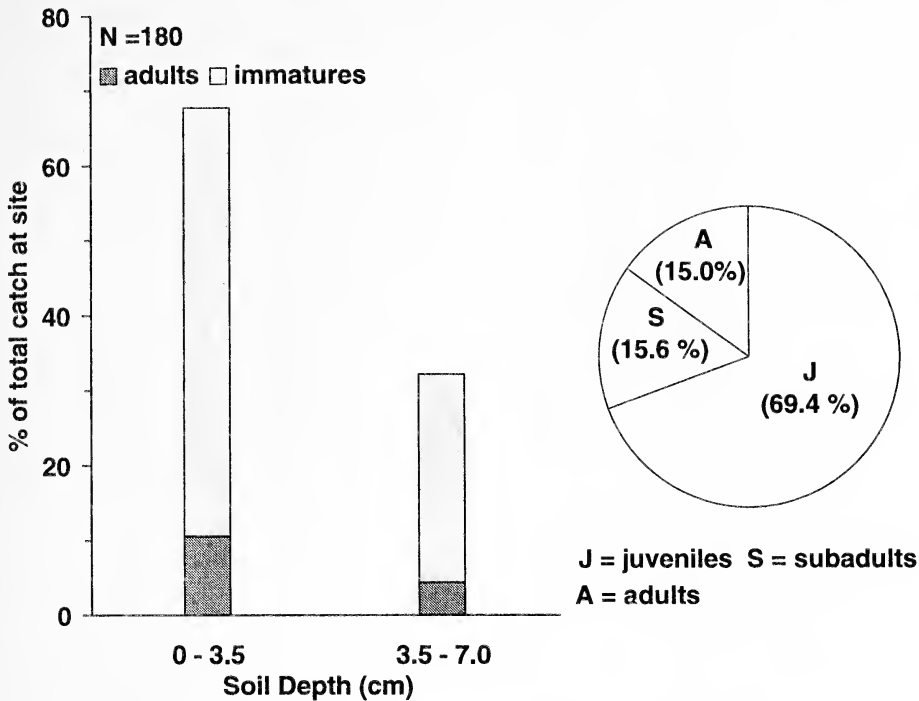


Figure 2.—Distribution of *Surazomus brasiliensis* in the soil according to soil depth, and percentage of developmental stages in a primary upland forest near Manaus. (Total catch = 100%) Samples taken monthly at 0–3.5 and 3.5–7 cm depths over a 12 month period. (N = total number of specimens).

by *Surazomus brasiliensis* (body length ≤ 4.3 mm without flagellum; cf. Kraus & Beck 1967; Reddell & Cokendolpher 1995) and an undescribed species (Reddell & Cokendolpher 1999) of a new genus (96% and 4% of the total catch, respectively).

A total of 193 schizomids was collected. Out of these, 99% could be identified to their developmental stages. Schizomids were mostly found in the soil and never caught on tree trunks or in the canopy. Only three specimens (adults of *S. brasiliensis*), were captured in pitfall traps inside the ground photo-elector, while active on the soil surface. Schizomids represented 0.4% of the total arthropods extracted from soil samples within 12 months if Acari and Collembola are omitted (Morais 1985) and $\leq 0.1\%$ when they are included (Adis unpubl. data). The abundance of Schizomida in 0–7 cm soil depth was higher than that of the Palpigradi (455 vs. 351 ind/m²), whereas abundance of the Thelyphonida (7 ind/m²) was much lower (corrected data of Fig. 1 in Adis *et al.* 1997b). This is also consistent for the dominant species in each order (Fig. 1). An average abundance of 37.5 ± 16.8

schizomids/m²/month was recorded in 0–7 cm soil depth (*S. brasiliensis*: 36.1 ± 16.8 ind/m²/month; new genus, new species: 1.4 ± 1.7 ind/m²/month).

Most specimens of *S. brasiliensis* inhabited the organic soil layer (Fig. 2: 0–3.5 cm) and a few (32%) the mineral subsoil (3.5–7.0 cm depth). About 70% (25.0 ± 13.7 ind/m²/month) of the total catch was represented by juveniles (Fig. 2), and 15% each by subadults and adults (5.5 ± 4.1 and 5.5 ± 4.6 ind/m²/month, respectively). Sex ratio of adult males to females was 1:2.4 but instars of juveniles could not be sexed. No significant difference was found for the cephalothorax length between subadult males and subadult females (χ^2 test: $P < 0.05$).

The monthly abundance of juveniles in *S. brasiliensis* obtained from the organic soil layer (0–3.5 cm depth) was positively correlated with soil temperature ($17.6\text{--}26.6^\circ\text{C}$; average $23.8 \pm 2.4^\circ\text{C}$) (total catch: $r = +0.77097$, $P < 0.01$; $n = 12$). The total catches of specimens obtained during the dry season and the rainy season were similar: 48% versus 52%. However, there was no distinct

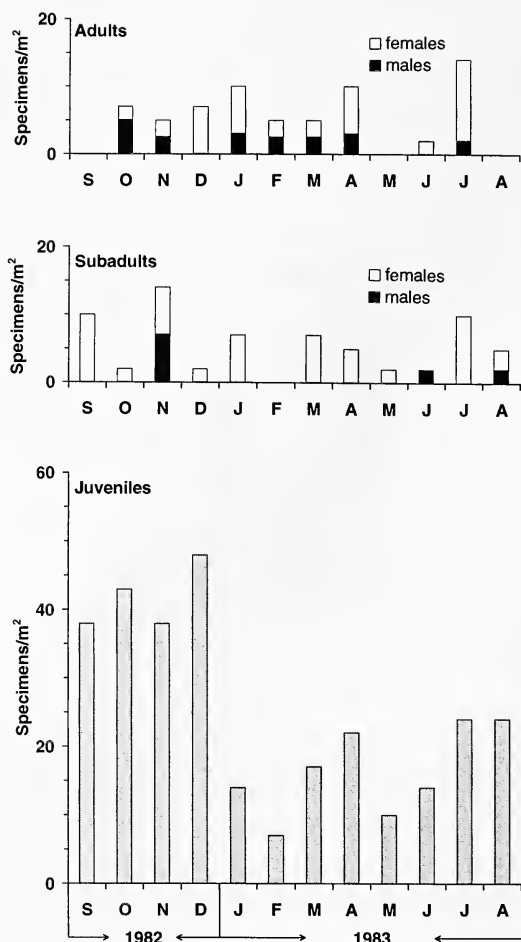


Figure 3.—Temporal occurrence of developmental stages of *Surazomus brasiliensis* in the soil (n/m² in 0–7 cm depth) of a primary upland forest near Manaus.

reproductive period because juveniles, in particular the first nymphal instar, as well as adults of both sexes, occurred throughout the year (Figs. 3, 4). These results indicate a plurioltine mode of life.

DISCUSSION

The low number of schizomids in samples from the ground photo-elector at Reserva Ducke indicates that these two species were rarely active on the soil surface. This conclusion is supported by another study at the reserve, in which apparently no schizomids were collected in 20 baited pitfall traps and in three or more ground photo-electors during a sample period of 12 months (Penny & Arias 1982).

The depth to which schizomids occur in the soil of the Central Amazonian upland forests is unknown. Our studies in various forest types near Manaus (Adis *et al.* 1987, 1989, 1997b, c) revealed their presence to a soil depth of 14 cm. The vertical distribution of *S. brasiliensis* is influenced by soil temperature in that catch numbers increased with rising temperatures.

Schizomids are easily mistaken for young spiders, particularly if their flagellum or front legs are missing. This might explain their “absence” in other studies on the Neotropical arthropod fauna in 0–30 cm soil depth (e.g., Harada & Bandeira 1994a,b; Macambira 1997; Serafino & Merino 1978).

Parthenogenesis has been reported for several schizomid species (Reddell & Cokendolpher 1995). In *S. brasiliensis* both sexes were present. However, more than twice as many females as males were captured. This was also observed in the euedaphic paligrad *Eukoenenia janetscheki* Condé 1993 from the same study site (Adis *et al.* 1997b). Predominance of females assures the continuation of a species. This was also found for three species of Symphyla from the primary upland forest at Reserva Ducke and from a secondary upland forest at Rio Tarumã Mirim near Manaus where the number of females was 2–4× higher than of males (Adis *et al.* 1997c).

Surazomus brasiliensis is the only Amazonian schizomid species for which observations on the biology are available (Kraus & Beck 1967). Beck (1968) observed that animals in whitesand soils at Reserva Ducke predominantly feed on Collembola and Symphyla. Prey is searched by actively running around in a jerky manner (*cf.* Humphreys *et al.* 1989; Sturm 1973) and exploring the surroundings with the long and highly mobile front legs, which also serve as tactile instruments. Once the prey is perceived, the pedipalps are used to seize and transfer it to the chelicerae where it is cut during longitudinal and vertical movements. After ingestion and deposition of the remains on the soil, animals often groom themselves, particularly the long front legs and the flagellar region which is reached by folding the abdomen over the cephalothorax (= opisthosoma and prosoma, respectively, in Beck 1968). The grooming procedure is concluded by cleaning the pedipalps and the chelicerae. A similar behavior was reported for

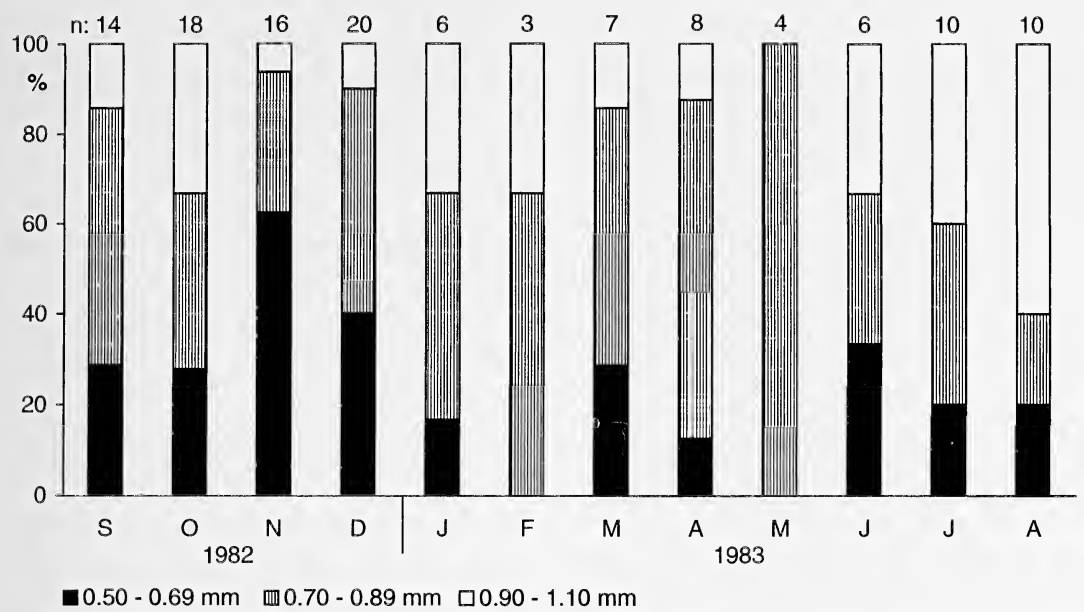


Figure 4.—Occurrence of three size classes in juveniles of *Surazomus brasiliensis* (based on the length of the cephalothorax). Specimens, obtained from 0–7 cm soil depth, presumably represent the three developmental stages in nymphs, apart from the subadult stage. (Number of specimens examined per month = 100%; 122 (97.6%) out of 125 juvenile specimens measurable).

two other schizomids: *Draculoides vinei* (Harvey 1988) from caves in western Australia (Humphreys *et al.* 1989) and for *Surazomus sturmi* (Kraus 1957) from the surroundings of Bogotá, Colombia (Sturm 1973). According to Beck, the mating behavior and indirect transfer of the spermatophore in *S. brasiliensis* is similar to that observed in *S. sturmi* (Kraus & Beck 1967; Sturm 1958, 1973).

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RELATIONSHIP OF HABITAT AGE TO PHENOLOGY AMONG GROUND-DWELLING LINYPHIIDAE (ARANEAE) IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT. Ground-dwelling Linyphiidae from eight South Carolina inner coastal plain habitats were sampled for one year using pitfall traps. Habitats formed an age gradient, from a field disturbed yearly and pine stands aged 5, 25 and 40 years, to xeric, mesic and hydric hardwoods (50–75 years) and an old-growth forest (200 years). Sixteen of the 55 trapped species were represented in sufficient numbers (n adults \geq number of sampling periods, 26) to examine patterns of correlation between phenology and habitat distribution. Half of the species are multivoltine, characterized by adults present throughout the year, continuous reproduction, and overlapping generations. Adult abundance of these species peaked during spring through autumn. Other species were univoltine, with adults present briefly, indicating synchronous reproduction and non-overlapping generations. Adult abundance of these species always peaked during winter months. This study examines relationships between observed voltinism patterns and characteristic habitat (distribution among the habitats) among the 16 most abundant species. Species from older habitats tend to be univoltine, whereas species inhabiting more recently disturbed habitats were more likely to be multivoltine. Stenochronous winter reproduction (univoltines) probably increases survivorship by limiting individuals' exposure to the harsh conditions of the southeastern summer during vulnerable periods of immaturity and reproduction. This phenological specialization appears optimal in this region except in frequently disturbed habitats, where rapid multivoltine reproduction is most advantageous.

Knowledge of cyclic temporal aspects of organisms' life cycles (phenology) is crucial for understanding population dynamics and community ecology, and lends realism to evolutionary and ecological hypotheses (Lieth 1974; Tauber & Tauber 1981). This basic data can be time-consuming to obtain, as it requires sampling a population repeatedly throughout the year, and phenology may vary geographically or from one year to the next. Although Linyphiidae is by far the most diverse spider family in North America (Coddington et al. 1990), little is known about the phenology of most North American species. This is particularly true of the ground-dwelling forms, whose small size (1–3 mm), high diversity (ca. 800 species in North America), and cryptic microhabitats within litter interstices, etc., make them difficult to observe in the field.

This paper is part of a research program examining life history variation among ground-dwelling Linyphiidae. As phenology

and other life history information is time-consuming to obtain, our goal is to determine the extent to which more easily obtainable kinds of information (such as the habitats used) are predictive of life history variation among ground-dwelling linyphiids. By understanding this, we may begin to apply information derived from careful phenological and laboratory studies to unstudied taxa as they are encountered in sampling.

Although linyphiids are most diverse in Northern Hemisphere mid-temperate latitudes and increasingly dominate spider assemblages farther north, they are still fairly diverse and form a conspicuous portion of spider assemblages in more southerly humid temperate regions, such as the southeastern Atlantic coastal plain of the United States (Draney 1997a, b). The present study examines species from the inner coastal plain of South Carolina (approximately 33° N).

Pitfall trapping during the course of this research yielded 55 species, of which 16 were

judged abundant enough to use in elucidating phenological patterns. Two general phenological patterns emerged (Draney 1997a): In about half of the species, the adults are eurychronous (present during most of the year); these species appear to be multivoltine, with overlapping generations and continuous reproduction. For all these species, adults trapped peaked during the warm season. The other species have stenochronous adults (present during only a short time during the year); these species appear to be univoltine in our region, with non-overlapping generations and a winter mating period. Although other phenological patterns doubtless exist in our region, these two general patterns of voltinism appear to be very common among ground-dwelling linyphiids in the southeastern US.

The objective of the present article is to examine the extent to which these observed voltinism patterns are correlated with the distribution of individuals of a species among our sampled habitats. It might be expected that habitats differing in time since last disturbance would favor different life history responses, corresponding to *r*- and *K*-selection models (Stearns 1992). Our sampled habitats were specifically selected to provide a wide gradient of habitat age, as measured by time since the soil/litter layer has been significantly disturbed (as by clear-cutting, burning, mowing, plowing, etc.). We expect that species occurring in younger, more recently disturbed habitats would be more likely to be multivoltine than species occurring in older, more permanent habitat types, for reasons discussed more fully in the Results and Discussion section.

METHODS

Study sites.—The study areas were located on the Savannah River Site (SRS), a 780 km² area adjacent to the Savannah River in Aiken, Allendale, and Barnwell Counties, South Carolina. SRS has been maintained by the US Department of Energy since 1951. Because a primary objective of this study was to determine whether habitat age is related to life history parameters of the linyphiid inhabitants, the primary criterion for site selection was to locate sites that vary widely in the frequency with which the soil stratum is disturbed. In addition, several relatively mature habitats of the same age but with different vegetative

communities were chosen. In all, eight areas were selected to represent the major terrestrial habitat types on the inner Atlantic coastal plain, here listed in order from the youngest, most recently disturbed to the oldest, least frequently disturbed habitat. For more detailed site information, see Draney (1997a). 1). Old Field: forb-grassland with *Opuntia* and lichen. Mowed or herbicided annually. 2). Young pines: 5 year-old plantation overgrown with *Rubus* and *Prunus* spp. 3). Medium pines: 25 year-old plantation with a sparse understory. 4). Mature Pines: 40 year-old volunteer pine stand with young oak and pine understory. 5). Scrub-Oak/Pines: 50–75 year-old xeric upland oak/pine stand. 6). Upland hardwood: 50–75 year-old mesic oak-hickory stand. 7). Riparian hardwood: 50–75 year-old hydric hardwood stand. 8). Riparian old growth: ca. 200 year-old pines within riparian hardwood stand.

Sampling methods.—A study area of about 1 ha was subjectively delimited to represent each selected habitat. A 0.25 ha (50 m × 50 m) plot was randomly located within this area, and 10 pitfall traps were randomly located within each plot. Pitfalls each consisted of an 8.5 cm diameter plastic cup buried with the lip flush to the soil surface, housed under a concrete building block (39 × 19 × 9 cm) propped up at one end by a 7 cm brick. Traps contained 4% formalin with a trace of detergent to decrease surface tension.

Traps were run continuously for a year (366 days, 1–4 May 1995 to 1–4 May 1996) and emptied at approximately biweekly intervals (11–17 days; mean = 14.0). At each of 26 sampling periods, all traps were collected from each of the eight sites. Contents were washed into a jar and the trap was refilled with formalin solution. Samples were sieved through a 250 µm mesh sieve to remove the formalin, and stored in 70% ethanol for subsequent identification. Nomenclature follows Buckle et al. (1993) and Platnick (1996). Voucher specimens of all species are deposited at AMNH and UGCA.

Data analysis.—Pitfall counts from each site during each trap period were expressed as number of organisms/140 trap-days (10 traps × 14 days), to correct for variable number of days per trap period, and to correct for the 22 traps lost to animal (dog or coyote) disturbance at the old field site.

A constraint of phenological data is that

Table 1.—Phenology and habitat indices of 16 ground-dwelling linyphiids from the South Carolina inner coastal plain. *n* = Number of adults trapped. *Is* = Index of seasonality. *Pm* = proportion of adults trapped at modal sampling period. *Ih* = Index of habitat range. *Ha* = Habitat age score. See text for explanation. Species are listed by voltinism (see Draney 1997a), and then by numbers of adults trapped.

Species	<i>n</i>	<i>Is</i>	<i>Pm</i>	<i>Ih</i>	<i>Ha</i>
Winter active, univoltine					
<i>Pelecopsidis frontalis</i> (Banks 1904)	199	2.6	0.307	3.64	4.18
unidentified species, cf. <i>Walckenaeria</i>	191	1.7	0.351	2.04	3.59
<i>Walckenaeria carolina</i> Millidge 1983	110	2.1	0.355	3.66	3.90
<i>Centromerus latidens</i> (Emerton 1882)	110	3.8	0.200	5.20	4.35
<i>Lepthyphantes sabulosus</i> (Keyserling 1886)	51	3.2	0.275	3.88	3.99
<i>Ceraticelus laetabilis</i> (L. Pickard-Cambridge 1874)	39	2.9	0.333	1.48	5.80
<i>Origanates rostratus</i> (Emerton 1882)	33	3.3	0.273	2.84	3.77
<i>Scylaceus pallidus</i> (Emerton 1882)	33	3.3	0.242	4.35	4.73
<i>Ceraticelus alticeps</i> (Fox 1891)	31	1.9	0.419	2.20	4.61
Eurychronous, multivoltine					
<i>Meioneta</i> sp. n. #1	805	9.5	0.083	2.22	2.48
<i>Meioneta</i> sp. n. #3	563	4.5	0.224	1.95	5.37
<i>Ceratinops crenatus</i> (Emerton 1882)	230	6.3	0.161	1.00	1.00
<i>Meioneta barrowsi</i> Chamberlin & Ivie 1944	72	4.5	0.181	2.91	3.46
<i>Eperigone maculata</i> (Banks 1892)	61	4.8	0.230	3.47	4.61
<i>Erigone autumnalis</i> Emerton 1882	32	5.8	0.125	1.84	1.43
<i>Meioneta micaria</i> (Emerton 1882)	31	3.7	0.226	3.22	3.90

many parameters are dependent on sample size. As the number of individuals sampled increases, the apparent temporal span of the species will tend to increase as well. Parameters pertaining to distribution of individuals across sampling periods were only calculated on categories (species, or sexes/stages within species) when the category sample size equaled or exceeded the number of sampling periods (*n* = 26; Table 1). Thus, phenological parameters were calculated only for 16 of the 55 linyphiid species trapped during this study (Draney 1997a).

We used several indices to compare the complex temporal and spatial distribution patterns of different species and sexes (Table 1). We calculated *Pm*, the proportion of adults trapped during the modal sampling period (that is, the period during which the maximal number of individuals of that species was trapped) as a simple indicator of each species' temporal distribution; higher proportions indicate more stenochronous populations. We also calculated an index of seasonality (*Is*; Curtis 1978) for each species. This index uses the proportion of individuals of a species captured in each month to determine how evenly the species is distributed throughout the year. As our sampling periods were biweekly in-

stead of monthly, the index was converted to a fraction and then multiplied by twelve to standardize the index to "months":

$$Is = 12[(1/\sum p_j^2)/s]$$

summed over all sampling periods, where *p_j* = proportion caught during sampling period *j*, and *s* = total number of sampling periods (always 26 in this study). The index varies from 12/*s* for a highly stenochronous species found only during one sampling period, to 12, for a completely eurychronous species evenly distributed across all sampling periods.

A modified index can be used to examine the distribution of spiders across sampled habitats. This index of habitat range, *Ih*, can be used to categorize species as eurytopic (occurring in many habitats) or stenotopic (occurring in a narrow range of habitat types):

$$I_h = 1/\sum p_k^2$$

summed over all habitats sampled, where *p_k* = proportion caught in habitat *k*. This index varies from 1 for a stenotopic species found in only one habitat, to the number of habitats sampled (in this case, 8). Both of the above indices assume that each sampling period or habitat is sampled equally, an assumption met

in the present study when the data are standardized to number/140 trap-days.

Because we are interested in the extent to which phenology and life history patterns may be predicted by habitat distribution, a habitat age score was calculated for each species. This score summarizes the characteristic habitat of each species with respect to habitat age, and is essentially a weighted average of a species' presence at each habitat, giving more weight to individuals found in older habitats: $P_1 = [(1n_1) + (2n_2) + (3n_3) + (4n_4) + (5n_5) + (5n_6) + (5n_7) + (6n_8)]/n_{\text{total}}$, where n_1 = Number of adults from old field, scored as 1 (disturbed yearly); n_2 = number from young pines, scored as 2 (ca. 5 years old); n_3 = number from medium pines, scored as 3 (ca. 25 years old); n_4 = number from large pines, scored as 4 (ca. 40 years old); n_5, n_6, n_7 = number from scrub-oak/pines, upland hardwoods, and riparian hardwoods, all scored as 5 (habitats were forested 40 years ago and so have been forested at least ca. 75 years); n_8 = number from old growth habitat, scored as 6 (forested for ca. 200 years); and n_{total} = sum of individuals from all sites. This species score varies from 1 to 6. For example, species found only at the most frequently disturbed habitat have a score of 1.00.

Single factor regression analyses were used to examine whether any habitat distribution indices (Ih or Ha) are related to phenological indices (Pm or Is) among the examined taxa.

RESULTS AND DISCUSSION

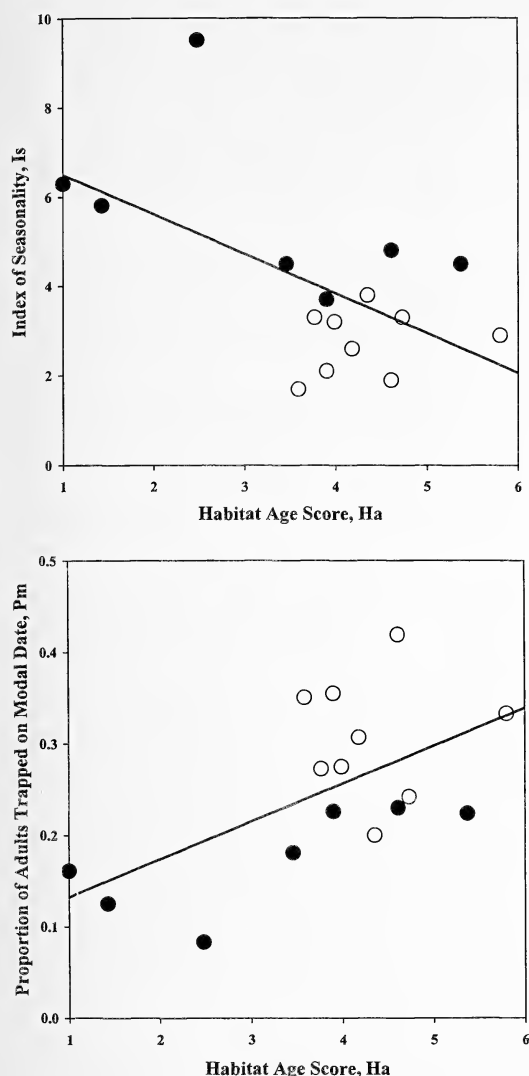
Species characteristically trapped at younger habitats tended to be more eurychronous and species at older habitats tended to be more stenochronous. Species habitat range (Ih) was not correlated with phenological indices, but the age of the habitats occupied by the species was correlated with phenology. Specifically, the adult index of seasonality, Is, was negatively correlated with habitat age score, Ha ($r^2 = 0.328$, $P = 0.0204$) and percent of adults at the species' modal date, Pm, was positively correlated with Ha ($r^2 = 0.345$, $P = 0.0167$; Table 1). These trends did not hold when the sexes were examined independently. This was probably due to the decrease in number of taxa examined: sample size was adequate ($n > 25$) to examine total adults (males and females combined) of 16 species, but males of only 11 species, and females of only five spe-

cies. It should be noted that Draney (1997a) found no evidence that the phenology patterns of individual taxa vary among the habitats (Draney 1997a), so it can be assumed that species are either univoltine or multivoltine within this region, regardless of the habitat they occupy.

In Figs. 1 and 2, species points in the scatterplots are labeled as multivoltine or univoltine, as determined by phenological indices, graphs of age/sex distribution over time, and other supporting evidence (Draney 1997a; Table 1). Among the species studied, those occurring mainly in younger, more frequently disturbed habitats (species with habitat age scores < 3.5) were all multivoltine, whereas species characteristically inhabiting older habitats were predominantly, but not exclusively, univoltine.

The apparent increased likelihood of finding eurychronous, multivoltine species in younger, less permanent habitats is consistent with the advantages which, we postulate, accompany this phenological strategy. Eurychronous spiders would be capable of reproducing opportunistically when the habitat is favorable or when they arrive at a favorable habitat. While the habitat remains favorable, continuous reproduction allows for individuals to maximize their instantaneous rate of reproduction (and thus, probably, their fitness). Finally, overlapping generations and the mixed age structure resulting from continuous reproduction mean that when the habitat changes, some individuals of the life history stage which is best able to survive by tolerance or dispersal should already be present. We postulate that these eurychronous species are phenological "generalists" with a flexible strategy that can result in successful reproduction even in unpredictable or impermanent habitats. It is interesting to note that Merrett's (1969) phenological study of 90 linyphiid species found that all eurychronous species were "common aeronauts," species commonly observed or collected ballooning.

Stenochronous species, conversely, appear to be phenological "specialists," finely adapted to completing various life history stages at specific times when conditions are most favorable, or to avoiding unfavorable conditions. All stenochronous species we examined are winter-reproducing, which seems to strengthen this specialization hypothesis. For



Figures 1–2.—Relationships between age of habitats in which linyphiid species were trapped, and indices of phenology. Each circle is data from all adults of one species (Table 1). Closed circles (●) are postulated to be multivoltine and open circles (○), univoltine (Draney 1997a). See text for r^2 and P values, and explanations of indices. 1, Negative correlation between habitat age score (Ha) and index of seasonality (Is); 2, Positive correlation between habitat age score (Ha) and proportion of adults trapped at modal sampling period (Pm).

three reasons, the mild southeastern US winter may be favorable for reproduction by ground-layer Linyphiidae. First, the cool, moist conditions that prevail in winter are probably more favorable both to survivorship of immatures, which are especially susceptible to

desiccation (based on pers. obs., MLD), and to the longevity of adults, which is negatively correlated with temperature and positively correlated with fitness in spiders (Li & Jackson 1996). Using such a stenochronous strategy, only adults would encounter the harsher summer conditions. In contrast, a eurychronous population would include many immatures during the summer. Second, Collembola, which are a major component of the prey of ground-dwelling linyphiids (Nyffeler & Benz 1988; Nentwig 1980, 1983, 1987; Alderweireldt 1994), are most abundant during the cool season (pers. obs. MLD). Third, we believe that both predation and competition for prey resources would be lower in the winter, since most other arthropod groups (including most spiders) are more active during the warm season. For organisms from a lineage that presumably evolved at higher latitudes (linyphiids are most diverse in mid-latitude temperate regions; van Helsdingen 1983), the southeastern US winter may indeed be a temporal “island” of favorable conditions, which may itself select for a stenochronous life cycle.

It appears that stenochronous winter reproduction is the predominant strategy for ground-dwelling linyphiids in this region, except in the younger habitats. We hypothesize that in such frequently disturbed habitats, the advantages of multivoltinism outweigh univoltinism's postulated advantage of avoiding the harsh conditions which ground-dwelling linyphiids would encounter during the southeastern summer.

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HOUSE SPIDERS OF KANSAS

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ABSTRACT: Spiders found in and around buildings may be divided into three categories: 1) true synanthropes, which can establish breeding populations in houses, seldom occur locally in the natural environment, and have broad ranges because they may be accidentally transported to new locations, 2) spiders which are seasonally abundant in natural habitats as well as in houses, but don't establish breeding populations in houses, 3) spiders which are rarely found in houses because they are locally rare or spiders that are locally common but are rarely found indoors. Fifteen species, including the venomous *Loxosceles relusa* and *Cheiracanthium mildei* are true synanthropes in Kansas. Category 2 contains 26 species, including the venomous species *Latrodectus hesperus*, *L. mactans*, and *L. variolus*. There are 33 species which are rarely found indoors in Kansas. Most species listed have been reported from buildings across the United States.

The interest of a homeowner is usually aroused when a spider is discovered inside the house. Since there are at least five species of Kansas spiders which can inflict bites serious enough to require medical attention, common questions that immediately come to mind are: "Is this spider venomous?", and "Can it hurt me?". Another concern is whether the house is "infested" with spiders, and what can be done to eliminate an infestation. In response to these questions, information on spiders found in and around houses, buildings, and other structures in Kansas was gathered from the author's personal collection and field notes, the spider collection of the University of Kansas Snow Entomological Museum, and the literature. Most records are from the Lawrence area in northeastern Kansas because this region has been more intensively studied than other parts of the state. The scientific names of spiders and their order in Tables 1–3 follow Platnick (1997). The relative prevalence of spiders in Kansas homes ranges from very common, common, occasional, uncommon to rare. Very common and common species are routinely found in buildings, while rare, uncommon and occasional species have been encountered on 1–5, 6–10, and 11–15 occasions, respectively.

Because Kansas is located at the center of the continental United States and contains a wide variety of natural habitats, including eastern deciduous forest and tallgrass and shortgrass prairies, it is the home of a diverse

array of plants and animals. The Kansas flora, for example, exhibits geographical affinities with eastern, southern, northern, western, and interior plant communities (Bare & McGregor 1970). Preliminary studies of the spider fauna of the state reveal a similar pattern (Fitch & Fitch 1966; Guarisco & Fitch 1995; Guarisco & Kinman 1990; Scheffer 1904, 1905). Therefore, many of the spiders encountered in Kansas homes can also be found in other parts of the continent. Some building-inhabiting species have even wider distributions, with populations on several continents.

House spiders can be conveniently divided into three categories. True synanthropes are associated with houses, can establish breeding populations in these locations, and usually have very wide distributions because they are often accidentally transported to new areas. They seldom occur locally in the natural environment. The second category includes species which are seasonally abundant in natural habitats and in houses. Although some may hibernate indoors, and the emergence of large numbers of spiderlings from an occasional eggsac may give the impression of an infestation, these species do not establish populations inside houses. The third category contains species which are rarely found in and around buildings. They are either common in natural situations and rarely frequent houses, or they are locally rare species. As Edwards & Edwards (1997) have indicated in their study of the spiders of rural delivery mailbox-

Table 1.—Synanthropic (associated with people) spiders in Kansas (Category 1). VC = very common, C = common, O = occasional, U = uncommon, R = rare.

Species	Distribution	Abundance
<i>Loxosceles reclusa</i> Gertsch & Mulaik 1940	US	VC
<i>Scytodes thoracica</i> (Latreille 1802)	Cosmopolitan	R
<i>Pholcus phalangioides</i> (Fuesslin 1775)	Cosmopolitan	C
<i>Spermophora senoculata</i> (Duges 1836)	Holarctic	R
<i>Dysdera crocata</i> C.L. Koch 1838	Cosmopolitan	O
<i>Oecobius cellariorum</i> (Duges 1836)	US, Europe	O
<i>Octonoba sinensis</i> (Simon 1880)	eastern US & Orient	O
<i>Achaeearanea tepidariorum</i> (C.L. Koch 1841)	Cosmopolitan	VC
<i>Steatoda triangulosa</i> (Walckenaer 1802)	Cosmopolitan	VC
<i>Tegenaria domestica</i> (Clerck 1757)	Cosmopolitan	C
<i>Amaurobius ferox</i> (Walckenaer 1830)	eastern US, Europe	O
<i>Cheiracanthium mildei</i> L. Koch 1864	US, Europe, north Africa	C
<i>Urozelotes rusticus</i> (L. Koch 1872)	Cosmopolitan	R
<i>Salticus scenicus</i> (Clerck 1757)	N. & S. America, Europe, north Africa	U
<i>Sitticus fasciger</i> (Simon 1880)	North America, Asia	R

es in Massachusetts, eventually individuals of all local species will be found in or around buildings. In addition to these three categories, alien species have been occasionally found in Kansas. These species are usually found in produce, such as bananas, and seldom establish breeding populations.

RESULTS

The list of true synanthropic spiders in Kansas presently contains 15 species (Table 1). The bites of two of these, *Loxosceles reclusa* (Sicariidae) and *Cheiracanthium mildei* (Miturgidae) can produce necrotic lesions that require medical attention (Gorham 1968; Spielman & Levi 1970), and the former is often present in large numbers in Kansas buildings. A sticky trap survey in the University of Kansas Museum of Natural History yielded 231 spiders in a two year period, 46.7% of these were *L. reclusa*. Two very common species occasionally play beneficial roles in houses. *Achaeearanea tepidariorum* (Theridiidae) was observed preying upon the lone star tick, *Amblyomma americanum* (Linnaeus) (Acarina: Ixodidae), and *Steatoda triangulosa* (Theridiidae) fed upon the brown recluse, *L. reclusa* (Guarisco 1991). Studies in New Zealand revealed that *Pholcus phalangioides* (Pholcidae) actively invades spider webs and preys upon its occupants (Jackson & Brassington 1987).

There are approximately 26 spider species which are seasonally abundant in natural en-

vironments and edificarian habitats (Table 2). The bites of *Herpyllus ecclesiasticus* (Gnaphosidae) (Majeski & Durst 1975), *Argiope aurantia* (Argiopidae) (Gorham & Rheney 1968), *Trachelas tranquillus* (Corinnidae) (Oehler 1971; Uetz 1973), and *Phidippus audax* (Salticidae) (Gorham 1968) have produced mostly local reactions; however, those of black widow spiders (*Latrodectus* sp.) can have much more serious consequences (White et al. 1995). In Kansas, black widows are sometimes discovered in outbuildings, garages and carports.

Mimetes puritanus (Mimetidae) and *M. notius* are specialized spider predators which are occasionally found on house eaves near or within host webs. *Euryopis limbata* (Theridiidae) occurs on walls and eaves of houses where females produce semicircular, tufted eggsacs. Two Kansas feeding records and observations elsewhere in its range (Archer 1946; Carico 1978) indicate this species' diet consists of ants. *Larinioides cornutus* (Argiopidae) and *L. patagiatus* build orbwebs on buildings and bridges near water. The large orbwebs of *Argiope aurantia*, *A. trifasciata* (Argiopidae), and *Neoscona crucifera* (Argiopidae) attract attention when located on porches and windows. The large fishing spider, *Dolomedes tenebrosus* (Pisauridae) is often found in sheds, basements and houses. Funnelweb weavers (*Agelenopsis* sp.) are of-

Table 2.—Seasonally common spiders in Kansas homes (Category 2). VC = very common, C = common, O = occasional, U = uncommon, R = rare.

Species	Distribution	Abundance
<i>Mimetus notius</i> Chamberlin 1923	eastern US	O
<i>Mimetus puritanus</i> Chamberlin 1923	eastern US	O
<i>Euryopis limbata</i> (Walckenaer 1841)	eastern US, Canada	O
<i>Latrodectus hesperus</i> Chamberlin & Ivie 1935	western US, Israel	O
<i>Latrodectus mactans</i> (Fabricius 1775)	North America	O
<i>Latrodectus variolus</i> Walckenaer 1837	eastern US, Canada	U
<i>Steatoda borealis</i> (Hentz 1850)	US, Canada, Alaska	O
<i>Theridion murarium</i> Emerton 1882	North America	C
<i>Argiope aurantia</i> (Lucas 1833)	North America to Costa Rica	O
<i>Argiope trifasciata</i> (Forsk. 1775)	Cosmopolitan	O
<i>Larinioides cornutus</i> (Clerck 1757)	Holarctic	VC
<i>Larinioides patagiatus</i> (Clerck 1757)	Holarctic	O
<i>Neoscona crucifera</i> (Lucas 1839)	North America, Canary Isl.	VC
<i>Hogna carolinensis</i> (Walckenaer 1805)	southern Canada, US	U
<i>Dolomedes tenebrosus</i> Hentz 1843	eastern US, Canada	C
<i>Agelenopsis naevia</i> (Walckenaer 1841)	US, Canada	VC
<i>Agelenopsis pennsylvanica</i> (C.L. Koch 1843)	US	VC
<i>Hibana gracilis</i> (Hentz 1847)	eastern US, Canada	C
<i>Elaver excepta</i> (L. Koch 1866)	eastern US, West Indies	O
<i>Castianeira variata</i> Gertsch 1942	eastern US, southern Canada	U
<i>Trachelas tranquillus</i> (Hentz 1847)	eastern US, southern Canada	O
<i>Herpyllus ecclesiasticus</i> Hentz 1832	North America	C
<i>Philodromus vulgaris</i> (Hentz 1847)	Holarctic	VC
<i>Maevia inclemens</i> (Walckenaer 1837)	US, Canada	C
<i>Phidippus audax</i> (Hentz 1845)	US, Canada	VC
<i>Platycryptus undatus</i> (De Geer 1778)	North & Central America	VC

ten located in corners, windows, and porches, while *Hibana gracilis* (Anyphaenidae), *Elaver excepta* (Clubionidae), and *Philodromus vulgaris* (Philodromidae) occur most often on ceilings and walls. The robust, hairy jumping spider, *Phidippus audax*, is often mistaken for a black widow by the homeowner because of its coloration.

The last category of spiders includes 33 species which occur in natural habitats and have rarely been found in or on buildings in Kansas (Table 3). Further investigation, especially in other sections of the state, would undoubtedly add species to this list. Two alien species have been found in northeastern Kansas. A tropical spider belonging to the genus *Cupiennius* (Ctenidae) was discovered in a produce shipment at the local community mercantile (Cutler pers. comm.). An adult female *Hibana cambridgei* (Bryant 1931) (Anyphaenidae) was found inside a Lawrence, Kansas residence. The owner may have acci-

dentally imported this spider from Arkansas when returning from a weekend trip.

DISCUSSION

The present study provides baseline data concerning house spiders in northeastern Kansas. The 15 synanthropic species and most of the seasonally common species found in northeastern Kansas homes have been reported from houses across the United States (Cutler 1973; Kaston 1983). *Amaurobius ferox* (Amaurobiidae) (Guarisco 1989), *Scytodes thoracica* (Scytodidae), *Cheiracanthium mildoi* (Guarisco 1991), and *Sitticus fasciger* (Salticidae) were first found in the Lawrence area in the late 1980s. Today, *C. mildei* is one of the most common local house spiders. Since its arrival in North America during the late 1940s (Bryant 1951), this old world species has spread from Boston and New York to southern Ontario, Illinois, California, and Alabama (Dondale & Redner 1982), and has re-

Table 3.—Spiders of rare occurrence in/on Kansas homes (Category 3).

Species	Distribution
<i>Mimetus epeiroides</i> Emerton 1882	eastern US
<i>Theridion goodnightorum</i> Levi 1957	western US
<i>Stemonyphantes blauveltae</i> Gertsch 1951	US, Canada
<i>Araneus pegnia</i> (Walckenaer 1841)	US to Ecuador, Jamaica
<i>Hogna helluo</i> (Walckenaer 1837)	US, Canada
<i>Pirata</i> sp.	
<i>Rabidosa punctulata</i> (Hentz 1844)	US
<i>Schizocosa ocreata</i> (Hentz 1844)	North America
<i>Pisaurina dubia</i> (Hentz 1847)	US
<i>Pisaurina mira</i> (Walckenaer 1837)	US, Canada
<i>Agelenopsis oklahoma</i> (Gertsch 1936)	US
<i>Anyphaena fraterna</i> (Banks 1896)	US
<i>Castianeira descripta</i> (Hentz 1847)	US, Canada
<i>Castianeira variata</i> Gertsch 1942	US, Canada
<i>Drassyllus lepidus</i> (Banks 1899)	US
<i>Drassyllus novus</i> (Banks 1895)	US, Canada
<i>Sergiolus montanus</i> (Emerton 1890)	North America
<i>Zelotes hentzi</i> Barrows 1945	US, Canada
<i>Zora pumila</i> (Hentz 1850)	US
<i>Philodromus keyserlingi</i> Marx 1889	US, Canada
<i>Philodromus marxi</i> Keyserling 1884	US
<i>Thanatus formicinus</i> (Clerck 1757)	Holarctic
<i>Thanatus rubicellus</i> Mello-Leitao 1929	US, Canada
<i>Bassaniana versicolor</i> (Keyserling 1880)	North America
<i>Misumenops oblongus</i> (Keyserling 1880)	Canada to Guatemala
<i>Xysticus auctificus</i> Keyserling 1880	US, Canada
<i>Xysticus ferox</i> (Hentz 1847)	US, Canada

Table 3.—Continued

Species	Distribution
<i>Xysticus texanus</i> Banks 1904	US, Mexico
<i>Habrocestum pulex</i> (Hentz 1846)	US, Canada
<i>Phidippus insignarius</i> C.L. Koch 1846	US
<i>Phidippus putnami</i> (Peckhams 1883)	US, Mexico
<i>Phidippus whitmani</i> (Peckhams 1909)	US, Canada
<i>Tutelina elegans</i> (Hentz 1846)	US

placed the native *C. inclusum* (Hentz 1847) (Clubionidae) in houses in the northeastern United States (Gertsch 1979). The mobility of today's society has hastened the spread of synanthropic spiders. Other notable instances of spiders being found well beyond their native ranges include, the western black widow (*L. hesperus*) and the brown recluse (*Loxosceles reclusa*) in Maine (Jennings & McDaniel 1988; McDaniel & Jennings 1983). The native *Steatoda borealis* (Theridiidae) has been displaced by the European species, *S. bipunctata* (Linnaeus 1758), in buildings in the northeastern United States (Nyffeler et al. 1986). Recent surveys of the spider fauna of Cape Cod, Massachusetts revealed the presence of two possible European immigrants, *Trochosa ruricola* (De Geer 1778) (Lycosidae) and *Lepthyphantes tenuis* (Blackwall 1852) (Linyphiidae) (Edwards 1993).

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SPIDER AND HARVESTMAN COMMUNITIES ALONG A GLACIATION TRANSECT IN THE ITALIAN DOLOMITES

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ABSTRACT. Arachnid communities of alpine grassland, of scree and woodlands near the timberline and of the nival zone have been compared along a transect from the northern to the southern border of the Dolomites. The region is zoogeographically interesting because of differences of the ice cover during glaciation, which was less severe in the southern area. Along the whole transect spider communities in grasslands and at the timberline zone show approximately the same composition. Endemic species, e.g., *Harpactea grisea* (Canestrini 1868), *Amaurobius ruffoi* Thaler 1990, *Coelotes mediocris* Kulczynski 1887, *Cybaeus intermedius* Maurer 1992 and *Eudasylobus ligusticus* Roewer 1923 occur mostly on the southernmost station, which remained free of ice. Re-immigrants over short distance are scarce, e.g., *Coelotes mediocris* at Passo Rolle and *Coelotes solitarius* L. Koch 1868 in the Puez area. Endemic species were not found in the alpine grassland of the northern Dolomites, which suggests severe impact of glacial events on the local fauna. Central alpine species, i.e., *Erigonella subelevata* (L. Koch 1869), *Metopobactrus nadigi* Thaler 1976, *Meioneta orites* (Thorell 1875), *Pardosa blanda* (C.L. Koch 1833) and *Pardosa mixta* (Kulczynski 1887) are still present at the southernmost boundary of the Alps. Nunataks in the northern and central area of the Dolomites allowed speciation effects within the nival fauna: *Lepthyphantes brunneri* Thaler 1984, *Lepthyphantes merretti* Millidge 1974, *Megabunus armatus* (Kulczynski 1887). Further zoogeographically interesting records are *Cryphoea nivalis* Schenkel 1919 and *Xysticus bonneti* Denis 1938.

RIASSUNTO. È stata studiata la composizione della fauna aracnologica della zona subalpina, alpina e nivale lungo un transetto che parte dalle Dolomiti settentrionali (Parco Naturale Puez-Odle) e porta fino al bordo meridionale delle Alpi (Monte Grappa). Il versante meridionale delle Alpi è di grande importanza ai fini di studi zoogeografici, essendo queste regioni in parte rimaste libere dai ghiacciai durante le epoche glaciali. Sul Monte Grappa sono state riscontrate più specie endemiche p.es. *Harpactea grisea* (Canestrini 1868), *Amaurobius ruffoi* Thaler 1990, *Coelotes mediocris* Kulczynski 1887, *Cybaeus intermedius* Maurer 1992 e *Eudasylobus ligusticus* Roewer 1923. Alcune specie reimmigranti a breve distanza hanno riconquistato parti delle Dolomiti raggiungendo regioni più a nord: *Coelotes mediocris* Kulczynski 1887 è stato catturato anche a Passo Rolle, *Coelotes solitarius* L. Koch 1868 anche nel Parco Naturale Puez-Odle. Specie endemiche sembrano essere assenti nella prateria alpina delle Dolomiti settentrionali, dimostrando l'effetto distruttivo dei ghiacciai sulla fauna del suolo. In questa zona si possono trovare specie endemiche sulle cime più alte rimaste libere dai ghiacciai: *Lepthyphantes merretti* Millidge 1974, *Lepthyphantes brunneri* Thaler 1984 e *Megabunus armatus* (Kulczynski 1887). Altre specie rare e di notevole interesse zoogeografico catturate nell'ambito di questo studio sono *Cryphoea nivalis* Schenkel 1919 e *Xysticus bonneti* Denis 1938. È particolarmente sorprendente la presenza sul Monte Grappa di specie tipiche delle Alpi centrali che sembrano spingersi fino al bordo più meridionale delle Alpi, p.es. *Erigonella subelevata* (L. Koch 1869), *Metopobactrus nadigi* Thaler 1976, *Meioneta orites* (Thorell 1875), *Pardosa blanda* (C.L. Koch 1833) e *Pardosa mixta* (Kulczynski 1887).

The southern Alps are interesting for zoogeographical research. During glaciation periods most of the Alps were covered with a thick ice layer (Kleibelsberg 1935; Husen 1987), but ice-free conditions (massifs de refuge) along the southern and south-eastern border made survival of animal and plant species possible (Holdhaus 1954). A few species also survived on summits rising above the ice shield (nunataks, Janetschek 1956). Ice-free

regions played an important part in differentiation of new species as well as in recolonization after glaciation. Therefore widely distributed faunal elements are present in the central Alps, whereas in the southern Alps also endemic species occur. Thaler (1976) recognized the main families which form endemic species on the southern border of the Alps: Dysderidae, Linyphiidae, Agelenidae and Amaurobiidae. Maurer (1982a) and Maurer &

Thaler (1988) studied living conditions in refugial areas and discussed the possible duration of speciation and migration.

Still little is known about spider communities living in the Dolomites. Koch (1876) and Kulczynski (1887) presented the first lists of the arachnids from this area. Further results concerning spiders or harvestmen of the Dolomite region were published by Janetschek (1957), Denis (1963) and Marcellino (1988). Marcuzzi (1956, 1975) provided general surveys of the fauna of the Dolomites. Noflatscher (1996) and Hellrigl (1996) summarized the spider and harvestman fauna of the South-Tyrol territory, including the northern part of the Dolomites. Lists of the spiders and harvestmen of northern Italy were given by Pesarini (1994) and Chemini (1994). Recently the spider fauna of the Puez region was studied by Zingerle (1997).

This paper compares arachnid communities from sites near the timberline, from alpine grasslands and from nival habitats along a transect between the northern Dolomites and the southern border of the Alps. It is part of the results of a larger study on the spider fauna of the Dolomites performed by the author.

METHODS

Study sites.—The study sites are situated in the northeastern corner of Italy, about 60 (Monte Grappa) to 140 km (Puez Nature Park) north of Venice in the regions Veneto and Trentino-South Tyrol (Fig. 1). The Dolomite Mountains are mainly composed of limestone and dolomite rock. Several summits rise up to more than 3000 m, the highest elevation is Mount Marmolada with 3342 m. Different forest types can be found due to decreasing rainfall and mediterranean influence between the southern border of the Dolomites and the central Alps. In southern sites the timberline occurs at 1700 m elevation and rises continuously up to 2300 m towards the north. In the timberline zone of the southern Dolomites mostly spruce and beech forest (*Picea abies*, *Fagus sylvatica*) are found; in northern sites larch (*Larix decidua*), cembra-pine (*Pinus cembra*) and mountain pine (*Pinus mugo*) exist. Ditches and humid places are mostly covered by associations of *Alnus viridis* and of *Salix* spp. Alpine grasslands on limestone and dolomite rock are dominated by *Carex sempervirens* and *Sesleria albicans*. On bare rocks

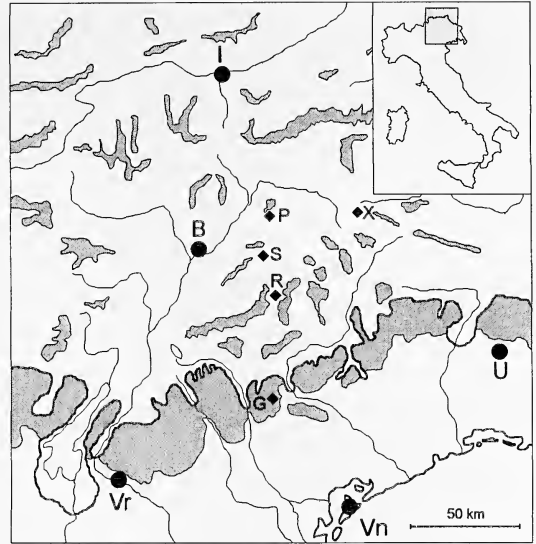


Figure 1.—Map showing position of the sampling areas in the Dolomites (Northern Italy) and ice-cover situation during glaciation (according to Klebelsberg 1935). Shaded area indicates ice-free regions on the border of the south-eastern Alps and nunataks (see text). Study sites: G = Monte Grappa (MG); P = Puez Nature Park (PU); S = Passo Sella (SE); R = Passo Rolle (RO); X = Sesto/Sexten Nature Park (SX). Main Cities in the vicinity of the study areas: B = Bolzano (Bozen); I = Innsbruck; U = Udine; Vn = Venice; Vr = Verona.

of the mountain tops there grow patches of mosses and grasses, like *Carex firma* and *Carex rupestris*. For a general view of the area, see Fig. 2. Five study areas were selected (see Fig. 1): *Monte Grappa*, elevation 1775 m, 45°55'N, 11°49'E, at the border between the Provinces Belluno, Vicenza and Treviso. *Passo Rolle*, Paneveggio Pale-S. Martino Nature Park, elevation 1970 m, 46°18'N, 11°48'E, Province Trento. *Passo Sella*, elevation 2244 m, 46°30'N, 11°48'E, at the border between Provinces Trento and South-Tyrol. *Puez Nature Park*, Antersasc Valley, elevation 2000 m, 46°37'N, 11°52'E, Province South-Tyrol. *Sesto/Sexten Nature Park*, Gsell area, elevation 2000 m, 46°40'N, 12°22'E, Province South-Tyrol.

Collection methods.—In each of the five study areas mentioned above, three habitats types (grassland, scree and forest at the timberline) were sampled by pitfall traps. Four covered traps containing a formalin/water solution and a small amount of detergent were



Figure 2.—Typical landscape of the Dolomites in the vicinity of Passo Rolle (RO). Alpine grasslands and subalpine woodlands sampled are visible on the left side of the photo, nival habitats on the right side.

placed a few meters apart from each other in each habitat. Altogether 15 sites were sampled by 60 traps. The traps remained in the area throughout a whole year and were emptied in intervals of 3–4 weeks during the vegetation period. In the Puez area sampling was carried out from Spring 1995 to Spring 1996, in the other areas from Spring 1997 to Spring 1998. For details about the traps see Zingerle (1997). The mean number of specimens per trap, number of species, diversity value ($^2\log$) according to Shannon-Weaver and family composition are given for each site.

Additionally, alpine and nival habitats were sampled during Summer 1995, 1996 and 1997 by hand collecting. This sampling technique is effective, due to the low species number in these habitats. Hand collecting was performed at the following localities: Puez (2600–2900 m), Sella (2900–3150 m), Sasso Lungo (Langkofel) (2700 m), Passo Falzarego (2400 m), Tofana (2950–3220 m), Cristallo (2400–2950 m), Sesto/Sexten (2450 m), Marmolada (3000–3300 m) and Pale di S. Martino (2700–3000 m).

Voucher specimens will be deposited in the Natural History Museum, Vienna (Austria) and in Naturmuseum Südtirol, Bozen (Italy).

RESULTS

Spiders and harvestmen of alpine grasslands and timberline zone.—The total material captured by pitfalls comprises 3640 adult specimens from 164 species and 15 families. The dominant families are: Linyphiidae (41% of specimens), Lycosidae (39%), Agelenidae (5%), Gnaphosidae (5%), Thomisidae (5%). Characteristics of the spider fauna found at each site are shown in Table 1.

On the whole transect family composition of spiders in grassland sites is approximately the same. In grasslands Lycosidae reach 48–74% of the total spiders. The most dominant species are *Pardosa blanda* (C.L. Koch 1833), *Pardosa oreophila* Simon 1937, *Alopecosa taeniata* (C.L. Koch 1848), *Pardosa riparia* (C.L. Koch 1833), *Trochosa terricola* Thorell 1856 and *Pardosa ferruginea* (L. Koch 1870). Fluctuation of abundance among these species in different areas is probably coincidental. The high abundance of Lycosidae in alpine grassland habitats is a well-known phenomenon. The secondmost important family is Linyphiidae (14–49%), mostly species with a preference for sites with an open canopy cover and little shade, like *Centromerus pabulator* (O.P.-

Table 1.—Structure of spider communities studied with pitfall traps in the Dolomites (Southern Alps, Italy) from spring 1995 to spring 1998. Abbreviations: x = mean number of individuals; S = number of species; H' = Shannon-Weaver diversity ($^2\log$). Percentages = number of specimens from a specific family ÷ the total number of spiders captured in a habitat during the whole sampling period. Habitats: G = alpine grassland; S = scree; T = forest sites near the timberline. Study areas: MG = Monte Grappa; RO = Passo Rolle; SE = Passo Sella; PU = Puez Nature Park (see also Zingerle 1997); SX = Sesto/Sexten Nature Park.

Habitat			Study areas				
			MG	RO	SE	PU	SX
G	x		98	102	80	79	93
	S		40	27	32	24	24
	H'		3.6	3.3	2.2	2.7	3.1
	Family	Lycosidae %	67	63	74	65	48
	composition	Linyphiidae %	20	14	18	19	49
		Gnaphosidae %	10	11	4	7	1
		Thomisidae %	1	11	1	7	0
		others %	2 (4 fam.)	1 (4 fam.)	3 (5 fam.)	2 (4 fam.)	2 (5 fam.)
S	x		32	10	26	14	25
	S		30	9	16	15	16
	H'		4.2	2.4	2.9	3.5	3.0
	Family	Thomisidae %	2	44	31	30	46
	composition	Linyphiidae %	24	39	42	24	23
		Lycosidae %	16	10	26	26	23
		Gnaphosidae %	29	2	0	9	0
		Dysderidae %	17	0	0	0	0
		Theridiidae %	0	0	0	7	1
		others %	12 (4 fam.)	5 (1 fam.)	1 (1 fam.)	4 (1 fam.)	7 (2 fam.)
T	x		35	65	37	115	99
	S		30	28	31	39	37
	H'		3.8	3.4	3.5	3.9	3.8
	Family	Linyphiidae %	75	75	46	55	76
	composition	Lycosidae %	9	14	42	12	10
		Agelenidae %	9	4	1	29	2
		Gnaphosidae %	4	1	9	2	1
		Theridiidae %	0	5	0	1	6
		others %	3 (5 fam.)	1 (2 fam.)	2 (2 fam.)	1 (3 fam.)	5 (3 fam.)

Cambridge 1875), *Tiso vagans* (Blackwall 1834) and *Bolyphantes alticeps* (Sundevall 1832). High numbers of Linyphiidae (e.g., in Sesto) occur in the proximity of a dense vegetation cover. Shannon-Weaver diversity in grasslands reaches values between 2.2 and 3.6. The harvestman *Eudasylobus ligusticus* Roewer 1923, endemic to the southern border of the Alps, occurs in grasslands on Monte Grappa. The absence of an endemic *Coelotes* species in my collection in grasslands of this area is quite interesting (Maurer 1982a, b).

Screes are generally characterized by lower numbers of individuals and species. High diversity values (e.g., Monte Grappa) are found, when the influence of adjacent habitats is

great. So the dominant thomisid species (*Xysticus lanio* C.L. Koch 1824, *Xysticus desidiosus* Simon 1875 and *Xysticus audax* (Schränk 1803)) also occur in grassland areas. Typical inhabitants of alpine scree are *Lepthyphantes variabilis* Kulczynski 1887, *Tiso aestivus* (L. Koch 1872), *Rugathodes bellicosus* Simon 1873 and *Pardosa nigra* (C.L. Koch 1834). In scree on Monte Grappa exist also endemic spiders, *Harpactea grisea* (Canestrini 1868) and *Amaurobius ruffoi* Thaler 1990, and the endemic harvestman *Eudasylobus ligusticus*. All these are invaders from the neighboring forests.

Forests near the timberline are dominated by linyphiid spiders, which reach 46–76% of

Table 2.—Presence (+) or absence (–) of zoogeographically interesting spider and harvestman species in alpine grassland and woodlands near the timberline collected by pitfall traps in the Dolomites (Southern Alps, Italy) from Spring 1995 to Spring 1998. Study areas: PU = Puez Nature Park; SX = Sesto/Sexten Nature Park; SE = Passo Sella; RO = Passo Rolle; MG = Monte Grappa.

Species	Study areas				
	PU	SX	SE	RO	MG
<i>Harpactea grisea</i> (Canestrini 1868)	–	–	–	–	+
<i>Amaurobius ruffoi</i> Thaler 1990	–	–	–	–	+
<i>Cybaeus intermedius</i> Maurer 1992	–	–	–	–	+
<i>Eudasylobus ligusticus</i> Roewer 1923	–	–	–	–	+
<i>Coelotes mediocris</i> Kulczynski 1887	–	–	–	+	+
<i>Coelotes solitarius</i> L. Koch 1868	+	–	–	+	–
<i>Metopobactrus nadigi</i> Thaler 1976	+	–	+	–	+
<i>Meioneta orites</i> (Thorell 1875)	+	–	+	–	+
<i>Pardosa blanda</i> (C.L. Koch 1833)	+	–	+	–	+
<i>Lepthyphantes</i> cf. <i>fragilis</i> (Thorell 1875)	+	+	+	+	–
<i>Troglohyphantes tirolensis</i> Schenkel 1950	+	+	+	+	–
<i>Pardosa mixta</i> (Kulczynski 1887)	+	–	+	+	+
<i>Erigonella subelevata</i> (L. Koch 1869)	+	+	+	+	+

the spiders collected there. In addition, a high abundance of Agelenidae was found. Timberline sites are interesting because at this ecotone species from forest and alpine habitats occur together. Accordingly Lycosidae are also quite numerous and amount to 42% of all individuals from these habitats. Species numbers are generally higher than in other habitats and the Shannon-Weaver diversity index reaches values between 3.4 and 3.9, indicating a “mixed” fauna. Typical and abundant species from forest sites, which occur in the timberline zone are *C. pabulator*, *Diplocephalus latifrons* (O. P.-Cambridge 1863), *Lepthyphantes monticola* (Kulczynski 1882), *Lepthyphantes jacksonoides* Helsdingen 1977, *Cybaeus tetricus* (C.L. Koch 1839) and *Cryphoeca silvicola* (C.L. Koch 1834); species from alpine grassland are *P. blanda*, *A. taeniata*, *P. orophila* and *P. riparia*. Endemic spiders and harvestmen collected on Monte Grappa are: *Amaurobius ruffoi*, *Coelotes mediocris* Kulczynski 1887, *Cybaeus intermedius* Maurer 1992 and *Eudasylobus ligusticus*. Remarkable is the occurrence of *C. mediocris* at timberline sites of Passo Rolle.

Hand catches in alpine and nival zones.—Spider and harvestman communities in these zones are mainly composed of few specialists which, however, occur abundantly. Thaler (1981, 1988) collected 27 spider species in the nival zone of the central Alps and 49 nival species on 58 summits of the eastern

Alps. In the present study a total of 29 spider (299 individuals) and 4 harvestman species (11 individuals) were collected on 16 summits of the Dolomites between 2400–3300 m elevation. Twenty-two of these species belong to Linyphiidae, 2 to Theridiidae, 2 to Thomisidae, 1 to Agelenidae, Lycosidae and Philodromidae, respectively. Several of these species collected in high numbers on most summits show a rather continuous distribution in the studied area. Only two of them, *Hilaira montigena* (L. Koch 1873) and *Erigone tirolensis* (L. Koch 1872), occur mainly in the nival zone, the rest, (e.g., *L. variabilis*, *Meioneta gulosa* (L. Koch, 1869), *Diplocephalus helleri* (L. Koch 1869) and *Oreonetides glacialis* (L. Koch 1872)) are also present in the alpine zone. The ballooning lowland species *Meioneta rurestris* (C.L. Koch 1836) also occurs frequently in the nival zone. The harvestmen (*Dicranopalpus gasteinensis* Doleschall 1852, *Mitopus glacialis* (Heer 1845) and *Megabunus armatus* (Kulczynski 1887)) occur in the nival and in the alpine zone, whereas *Ischyropsalis kollari* C.L. Koch 1839 is also present in the montane woodland. Furthermore, two endemic spider species (i.e., *Lepthyphantes merretti* Millidge 1974 and *L. brunneri* Thaler 1984) with a mainly nival distribution were found quite numerously at certain localities (see Table 3). The endemic harvestman *Megabunus armatus* was also collected several times. These species demonstrate that the highest

Table 3.—Presence (+) or absence (–) of zoogeographically interesting spider and harvestman species in the alpine zone and the nival zone of the Dolomites (Southern Alps, Italy) collected by hand during Summer 1995, 1996 and 1997. Sampled localities: SE = Sella; PU = Puez; MA = Marmolada; PA = Pale di S. Martino; PF = Passo Falzarego; SL = Sasso Lungo/Langkofel; TO = Tofane; SX = Sesto/ Sexten; CR = Cristallo.

Species	Sampled localities									
	SE	PU	MA	PA	PF	SL	TO	SX	CR	
<i>Lepthyphantes merretti</i> Millidge 1974	+	+	+	+	–	–	–	–	–	
<i>Lepthyphantes brunneri</i> Thaler 1984	–	–	–	–	–	–	+	+	+	
<i>Megabunus armatus</i> (Kulczynski 1887)	+	+	–	–	+	+	+	–	–	
<i>Cryphoea nivalis</i> Schenkel 1919	–	–	–	+	–	–	–	–	–	
<i>Xysticus bonneti</i> Denis 1938	–	–	–	–	+	–	–	–	–	

summits of the Dolomites were spared by glaciation events, allowing speciation to take place. Two remarkable nival spiders species were captured only at one site each: *Cryphoea nivalis* Schenkel 1919 on Pale di S. Martino (2700 m) and *Xysticus bonneti* Denis 1938 in the vicinity of Passo Falzarego (2400 m).

DISCUSSION

The fauna of spiders and harvestman from the alpine and the timberline zone of the Dolomites shows a similar composition in the northern and in the southern area. Nevertheless, a few species indicate a minor impact of glaciation events in the border region and give evidence for peripheral isolation in the southern Dolomites (e.g., *Harpactea grisea*, *Amaurobius ruffoi*, *Cybaeus intermedius*, *Coelotes mediocris* and *Eudasylobus ligusticus*). Whether these species occur at northern sites or not depends on their capabilities to re-colonize the area after glaciation (see Table 2). Some species, like *H. grisea*, *A. ruffoi*, *C. intermedius* and *E. ligusticus*, seem to be restricted to the southernmost border, occurring exclusively on Monte Grappa. Others, (e.g., *Coelotes mediocris*), re-immigrated into the area up to Passo Rolle and show a higher mobility. *Coelotes solitarius* probably survived glaciation periods near the south-eastern border of the Alps; nevertheless it was found all the way up to the northernmost site, the Puez area. Populations of *Lepthyphantes* cf. *fragilis* (Thorell 1875) and *Troglohyphantes tirolensis* Schenkel 1950 were also influenced by glaciation, but further taxonomic work is needed to realize their precise status. Maurer (1982a, b) reported the occurrence of 10 species of the

Coelotes pastor-group from alpine grasslands between Liguria (Italy) and Slovenia, e.g., *C. pastor lessinensis* Maurer 1982 on Monti Lessini and *Coelotes alpinus* Polenec 1972 in the easternmost area. Species from this group were not found during this study. Remarkable is the presence of central-alpine spiders, (i.e., *Erigonella subelevata*, *Metopobactrus nadigi*, *Meioneta orites*, *Pardosa blanda* and *P. mixta*) at the southernmost limit of the Alps at Monte Grappa.

The nival fauna of the Dolomites demonstrates isolation effects and speciation on nunataks during glaciations. The endemic Linyphiidae *Lepthyphantes merretti* and *L. brunneri* were found on only a few summits, *L. brunneri* being distributed in the eastern and *L. merretti* in the western area of the Dolomites (see Table 3; Thaler 1988). The endemic harvestman *Megabunus armatus* is restricted to the south-eastern Alps where it lives on rocks above the timberline. The vicariance pattern in this genus in the Alps probably reflects the effects of glaciation (Martens 1978; Chemini 1985). The agelenid *Cryphoea nivalis* was previously known only from the Adamello and Brenta area in Italy and from the central Swiss Alps (Thaler 1978; Maurer & Hänggi 1990). The station in the Dolomites is probably close to its easternmost boundary of distribution. *Xysticus bonneti* is a rarely found species (Thaler 1981), which shows a very patchy distribution in the alpine zone of the western palearctic mountains.

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SALTICIDAE (ARACHNIDA, ARANEAE) OF ISLANDS OFF AUSTRALIA

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ABSTRACT. Thirty nine species of Salticidae from 33 Australian islands are analyzed with respect to their total distribution, dispersal possibilities and relations with the continental fauna. The possibility of the Torres Strait islands as a dispersal route for salticids is discussed.

The studies of island faunas have been the subject of zoogeographical and evolutionary research for over 150 years and have resulted in hundreds of papers, with the syntheses by Carlquist (1965, 1974) and MacArthur & Wilson (1967) being the best known.

Modern zoogeographical analyses, based on island spider faunas, began some 60 years ago (Berland 1934) and have continued ever since by, e.g., Forster (1975), Lehtinen (1980, 1996), Baert et al. (1989), Żabka (1988, 1990, 1991, 1993), Baert & Jocqué (1993), Gillespie (1993), Gillespie et al. (1994), Prószyński (1992, 1996) and Berry et al. (1996, 1997), but only a few papers were based on verified and sufficient taxonomic data.

The present contribution is mostly based on material collected by one of us (MZ) while visiting Queensland Museum (Brisbane), Australian Museum (Sydney), Western Australian Museum (Perth) and Australian National Insect Collection (Canberra). The main purposes of this paper are (1). To analyze the species composition in respect to their origin, total distribution and dispersal abilities; (2). To estimate the expansiveness of Australian continental faunas towards studied islands; (3). To evaluate the role of Torres Strait islands in faunistic exchange between Australia and New Guinea.

THE AREA

The islands are of coral, volcanic or continental origin and are (with few exceptions) located along the NE coast of Australia (Fig. 1). Their surfaces are rather flat, either barren or vegetated, mostly by *Eucalyptus*, wattles, palms and ferns. Few have developed rainforest or mangrove communities. Due to

ocean level fluctuations over the last 50,000 years, at least some islands have been submerged or formed land bridges with the continent (e.g., Torres Strait islands). All these circumstances and the human occupation make it rather unlikely for the majority of islands to have developed their own endemic salticid faunas.

When one of us (MZ) began research on the Australian and New Guinean Salticidae over ten years ago, close relationships between the faunas of these two regions were expected. Consequently, it was hypothesized that the Cape York Peninsula and Torres Strait islands were the natural passage for dispersal/expansion. In fact, the parts of this area covered with savannah and *Eucalyptus* forests do form such a passage zone within these habitats, but mostly in one direction—from Australia to South Papua, and no further north because of rainforest barrier. During glacial cooling, aridization and rainforest regression, habitats were further enhanced in favor of the Australian fauna. Thus, for northern (Oriental and New Guinean) rainforest dwellers, the Cape York Peninsula and Torres Strait islands should be treated as filters rather than a dispersal route.

THE SALTICIDS

Continental fauna—the source.—About 340 salticid species have been reported from Australia so far (Davies & Żabka 1989; Żabka 1990, 1991, unpubl. data). Of them 286 belong to 63 verified genera, others are classified as *incertae sedis*. Approximately 60% of species are endemic and these increase in number towards southern and central-western Australia. The long-term isolation of the con-

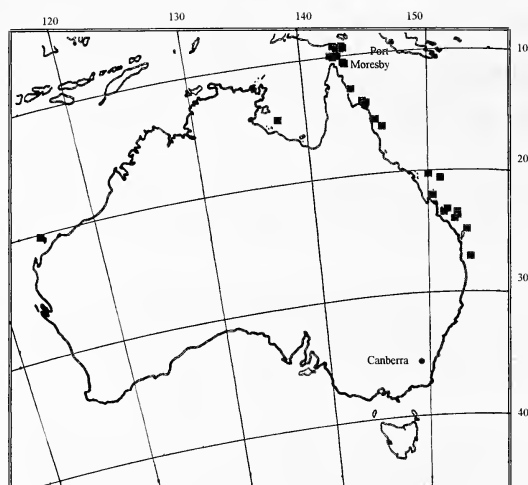


Figure 1: Map showing the geographical location of the analyzed islands along the coast of Australia (for detailed information see Table 1).

tinent and uniqueness of the Australian biota made the speciation so successful. Furthermore, inhabiting various *Eucalyptus* communities, remote desert and semi-desert areas and/or microhabitats (e.g., under bark, in leaf litter), particular species have biological and structural limitations to expansion. The second largest group of continental salticids, but smaller than expected especially in comparison with other spider families (Araneidae, Theridiidae, see Main 1981), is formed of tropical immigrants from the Oriental Region and New Guinea. They spread to north and north-eastern coastal rainforest remnants, and decrease in number to the south. Finally, the third group is made up of cosmopolitan/pantropical species, distributed by human activity.

Island fauna.—During the last ten years substantial progress has been made in studies of the Pacific island Salticidae (Žabka 1988; Prószyński 1992, 1996; Berry et al. 1996, 1997). In our research, we analyzed 39 species, though no island had more than eight species. Being aware of the limitations, we distinguish three groups of species (Tables 2, 3).

Group 1: The largest (24 species) is made up of Australian endemics. Although some of them have also spread to south Papua (savannah, *Eucalyptus* forests) they seem to be of Australian origin and belong to Australian endemic genera (*Abracadabrella*, *Astia*, *Holo-*

platys, *Ligurinus*, *Mopsus*, *Mopsolodes*, *Simaetha*, *Tauala*). Four species of this group (*Ergane cognata*, *E. insulana*, *Simaetha atypica* and *Tauala minutus*) are known exclusively from the islands. However, their endemic island status seems doubtful due to the young age of the inhabited islands.

Group 2: At least 11 species are of wide distribution, ranging from west Africa through Sri Lanka to western Pacific islands (in one case even to Hawaii) and belong to genera of alien (outside Australian) origin—usually SE Asian and New Guinean. *Cytaea plumbeiventris*, reported from 12 islands, was the most common here. This species can be found in gardens and parks of NE Queensland and as such has probably been dispersed by man. *Cosmophasis thalassina* has a similar biology and distribution, though it is less common (three islands).

Group 3: Four island species have cosmopolitan/pantropical distribution, and all live in human habitations and are spread by man.

Dispersal.—For the analyzed case two dispersal methods, aerodispersal and antropodispersal, should be considered. Rafting, though theoretically possible, is not discussed because of lack of published or other data regarding Salticidae.

Aerodispersal: Salticidae occupy various habitats, each providing different aerodispersal possibilities. Leaf-litter or bark dwellers, for instance, are poorer candidates for ballooning than those living in open areas, tree canopies or human habitats. Salticidae constitute only 1.5–7% of all spiders in aeroplankton (Horner 1975; Salmon & Horner 1977; Greenstone et al. 1987). It is widely known that juveniles are more effective ballooners than adults; and in our research they constituted 50.7% of all specimens which seems to support the aerodispersal hypothesis. Some indirect data from the analyzed area were provided by Žabka (1991) from tree canopies of NE Queensland. Amongst 70 specimens found there, the most common were representatives of *Tara*, *Simaethula*, *Opisthoncus*, *Prostheclina*. Except for the latter, those genera have also been recorded in our study. *Tara* and *Simaethula* have not been considered as identified to the genus (not species) level only. *Helpis minitabunda* (found in tree canopies) is spread from Australia and New Guinea to adjacent archipel-

Table 1.—Number of species recorded on individual islands.

Number of species	Island	Geographical location	
		S	E
8	Fitzroy	16°56', 146°00'	Queensland
8	Masthead	23°32', 151°43'	Queensland
7	Horn	10°37', 142°17'	Torres Strait
5	Heron	23°26', 151°55'	Queensland
4	Barrow	20°46', 115°24'	Western Australia
4	Lizard	14°40', 145°28'	Queensland
4	Motmot		
3	Cairncross West	11°15', 142°55'	Torres Strait
3	Hannibal East	11°36', 142°56'	Torres Strait
2	Campbell	9°34', 143°29'	Torres Strait
2	Darnley	9°35', 143°46'	Torres Strait
2	Fraser	25°22', 153°07'	Queensland
2	Friday	10°36', 142°10'	Torres Strait
2	Murray	9°56', 144°04'	Torres Strait
2	North West	23°18', 151°42'	Queensland
2	Pellew	15°31', 136°53'	Northern Territory
2	Pethebridge	14°44', 145°05'	Queensland
2	Stephens	9°31', 143°32'	Torres Strait
2	Thursday	10°35', 142°13'	Torres Strait
2	Tryon	23°15', 151°46'	Queensland
2	Yam	9°53', 143°45'	Torres Strait
1	Binstead	13°13', 143°33'	Queensland
1	Gannett Cay	21°59', 152°28'	Queensland
1	Little Fitzroy	16°55', 146°01'	Queensland
1	Low	22°03', 150°06'	Queensland
1	Moreton	27°11', 153°24'	Queensland
1	Percy	21°42', 150°20'	Queensland
1	Rocky	15°36', 145°21'	Queensland
1	Saibai	9°23', 142°40'	Queensland
1	Tana		
1	Wharton Reef	14°08', 144°00'	Queensland
1	Wilson	23°18', 151°55'	Queensland
1	Yorke	9°44', 143°25'	Torres Strait

agos and to New Zealand, and has also been found in our research.

Anthropodispersal: This way of dispersal is typical for species occupying human habitations, and their distribution is world-wide. Four such species (*Hasarius adansoni*, *Menemerus bivittatus*, *Plexippus paykulli*, *P. petersi*) are found on the islands. It is likely that also other island species (e.g., *Cytaea plumbeiventris*, *Cosmophasis thalassina*) can disperse this way.

CONCLUSIONS

Only 10% of all continental Australian salticid species are found on the analyzed islands, indicating they are either poorly studied, scanty in species and/or ecologically

inappropriate. Even some large continental genera are missing on the islands or are represented by single species only (Table 4). This supports the idea (quite obvious for resident Australian arachnologists) that the enormously diverse Australian spider/salticid fauna is largely the result of habitat variability and floristic diversity. The islands, being poor in plant communities, are mostly inhabited by eurytopic species. However, until the material is more complete, it is premature to reliably discuss such "island problems" as size effect, distance from the source of the fauna, island age, plant communities and topographic influence. For the majority of islands only one or two species are listed. Even for the richest (Fitzroy) only eight species are recorded. Of all

Table 2.—The distribution of species recorded on islands off Australia. WA = Western Australia, NT = Northern Territory, SA = South Australia, TAS = Tasmania, QLD = Queensland, NSW = New South Wales, NG = New Guinea, PNG = Papua New Guinea, C = central, M = middle, S = south, W = west, NE = north-east, E = east, N = north.

Species	Islands	Records in continental Australia				Other records
		WA	NT	QLD	NSW	
<i>Abracadabrella elegans</i>	Binstead			NE, E	E	
<i>Astia hariola</i>	Fraser			E	E	NG
<i>Bavia aericeps</i>	Horn, Campbell			NE		NG, C and W Pacific Archipelagoes
<i>Bianor maculatus</i>	Gannett Cay, Motmot			S	E	New Caledonia, Samoa, Vietnam
<i>Clynotis severus</i>	Yam, Horn	+		E	E	S PNG
<i>Cosmophasis bitaeniata</i>	Fitzroy			E	E	PNG, Aru Is.
<i>Cosmophasis micarioides</i>	Motmot			NE		
<i>Cosmophasis thalassina</i>	Cairncross West, Fitzroy, Hannibal East			N		Malay Arch., NG
<i>Cyrba ocellata</i>	Barrow, Masthead					from Africa to Oriental Region and Australia
<i>Cytaea mitellata</i>	Campbell					Aru Is., Yule Is., Sunda Arch.
<i>Cytaea frontaligera</i>	Darnley			E	N	PNG, Aru Is.
<i>Cytaea plumbeiventris</i>	Fitzroy, Hannibal East, Heron, Horn, Little Fitzroy, Lizard, Low, Masthead, Murray, Pethebridge, Stephens, Tryon			NE		Aru Is., PNG, New Mecklenburg
<i>Cytaea severa</i>	Barrow, Lizard, Masthead, Yam			+		
<i>Ergane cognata</i>	Pellew					
<i>Ergane insulana</i>	Pellew					
<i>Euryattus bleekeri</i>	Cairncross West, Fitzroy, Thursday			NE, M		NG, Ambon, Aru, Malaysia
<i>Evarcha infrastrata</i>	Horn			NE, E		
<i>Gangus longulus</i>	Motmot			+		
<i>Hasarius adansoni</i>	Heron, Masthead, North West, Percy, Wilson					Pantropical
<i>Helpis minitabunda</i>	Fitzroy			SE		
<i>Holoplatys colemani</i>	Lizard, Masthead			+	+	
<i>Holoplatys complanata</i>	Fitzroy, Masthead, Tryon	N		E		PNG
<i>Ligurinus bipenicilatus</i>	Fraser			+	+	
<i>Menemerus bivittatus</i>	Barrow, Heron, Masthead					Pantropical
<i>Mopsolodes australiensis</i>	Horn	+		N, NE, SE		
<i>Mopsus mormon</i>	Fitzroy, North West, Saibai			+	N	NG
<i>Opisthoncus abnormis</i>	Wharton Reef			+	+	
<i>Plexippus paykulli</i>	Hannibal East					Pantropical
<i>Plexippus petersi</i>	Thursday					Pantropical
<i>Servaea vestita</i>	Yorke			E	+	Tasmania
<i>Simaetha atypica</i>	Pethebridge	+				
<i>Simaetha robustior</i>	Stephen			NE		Aru
<i>Simaetha tenuidens</i>	Friday, Heron, Horn, Moreton			E		PNG
<i>Simaetha tenuior</i>	Barrow, Heron, Masthead			E		

Table 2.—Continued

Species	Islands	Records in continental Australia				Other records
		WA	NT	QLD	NSW	
<i>Tauala minutus</i>	Murray					
"Trite" <i>longula</i>	Cairncross West, Darnley, Motmot, Rocky			NE		
<i>Zenodorus arcipluvius</i>	Tana					New Hebrides
<i>Zenodorus metallescens</i>	Horn			E	E	
<i>Zenodorus orbiculatus</i>	Fitzroy, Fraser, Friday, Lizard			E	E	

39 species, three zoogeographic groups are distinguished: Australian endemics, Oriental and New Guinean immigrants, and cosmopolitan/pantropical elements. We hypothesize that no island endemics are found, unless confirmed by further research. Ballooning and man agency seem possible ways of dispersal; however, it is more likely that, at least some islands were colonized *via* past land bridges. The Torres Strait islands are the barrier for northern tropical (rainforest) species and the passage for southern savannah and *Eucalyptus* forest inhabitants.

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Table 3.—Island species and their zoogeographic distribution.

Australian endemics	Widely distributed	Cosmopolitan/pantropical
<i>Abracadabrella elegans</i>	<i>Bavia aericeps</i>	<i>Hasarius adansoni</i>
<i>Astia hariola</i>	<i>Bianor maculatus</i>	<i>Menemerus bivittatus</i>
<i>Clynotis severus</i>	<i>Cosmophasis bitaeniata</i>	<i>Plexippus paykulli</i>
<i>Cosmophasis micarioides</i>	<i>Cosmophasis thalassina</i>	<i>Plexippus petersi</i>
<i>Cytaea severa</i>	<i>Cyrba ocellata</i>	
<i>Ergane cognata</i>	<i>Cytaea frontalis</i>	
<i>Ergane insulana</i>	<i>Cytaea mitellata</i>	
<i>Evarcha infrastrata</i>	<i>Cytaea plumbeiventris</i>	
<i>Gangus longulus</i>	<i>Euryattus bleekeri</i>	
<i>Helpis minitabunda</i>	<i>Zenodorus arcipluvius</i>	
<i>Holoplatys colemani</i>	<i>Zenodorus orbiculatus</i>	
<i>Holoplatys complanata</i>		
<i>Mopsus mormon</i>		
<i>Ligurinus bipenicilatus</i>		
<i>Mopsolodes australiensis</i>		
<i>Opisthoncus abnormis</i>		
<i>Servaea vestita</i>		
<i>Simaetha atypica</i>		
<i>Simaetha robustior</i>		
<i>Simaetha tenuidens</i>		
<i>Simaetha tenuior</i>		
<i>Tauala minutus</i>		
"Trite" <i>longula</i>		
<i>Zenodorus metallescens</i>		

Table 4.—Island genera in comparison with the continental fauna (after Žabka 1991, unpubl.).

Australian genera	Number of species on	
	the Continent	the Islands
<i>Abracadabrella</i>	3	1
<i>Adoxotoma</i>	2	
<i>Afraflacilla</i>	5	
<i>Arasia</i>	2	
<i>Ascyltus</i>	1	
<i>Astia</i>	2	1
<i>Bavia</i>	3	1
<i>Bianor</i>	2	1
<i>Canama</i>	1	
<i>Clynotis</i>	1	1
<i>Cocalus</i>	1	
<i>Coccorchestes</i>	1	
<i>Copocrossa</i>	1	
<i>Cosmophasis</i>	6	3
<i>Cyrba</i>	1	1
<i>Cytaea</i>	5	4
<i>Damoetas</i>	1	
<i>Diolenius</i>	1?	
<i>Ergane</i>	—	2
<i>Euryattus</i>	4	1
<i>Evarcha</i>	1	1
<i>Frigga</i>	1	
<i>Gangus</i>	2	1
<i>Grayenulla</i>	5	
<i>Harmochirus</i>	1	
<i>Hasarius</i>	2	1
<i>Helpis</i>	3	1
<i>Holoplatys</i>	36	2
<i>Hypoblemum</i>	3	
<i>Jacksonoides</i>	7	
<i>Jotus</i>	1	
<i>Lauharulla</i>	1	
<i>Ligonipes</i>	4	
<i>Lycidas</i>	22?	
<i>Maratus</i>	7	
<i>Margaromma</i>	1	
<i>Megaloastia</i>	1	
<i>Menemerus</i>	2	1
<i>Mintonia</i>	1	
<i>Mopsolodes</i>	1?	1
<i>Mopsus</i>	1	1
<i>Myrmarachne</i>	10	
<i>Ocrisiona</i>	8	
<i>Omoedus</i>	1	
<i>Opisthonus</i>	31	1
<i>Palpeli</i>	2	
<i>Paraplatoides</i>	5	
<i>Plexippus</i>	2	2
<i>Portia</i>	1	
<i>Prostheclina</i>	1	
<i>Pseudomaevia</i>	1	
<i>Pseudosynagelides</i>	6	
<i>Rombonatus</i>	1	

Table 4.—Continued

Australian genera	Number of species on	
	the Continent	the Islands
<i>Servaea</i>	3	1
<i>Simaetha</i>	10	4
<i>Simaethula</i>	8	
<i>Sondra</i>	11	
<i>Tara</i>	3?	
<i>Tauala</i>	7	1
<i>Trite</i>	5?	1
<i>Zebraplatys</i>	4	
<i>Zenodorus</i>	14	3

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PSEUDOSCORPIONS IN FIELD MARGINS: EFFECTS OF MARGIN AGE, MANAGEMENT AND BOUNDARY HABITATS

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ABSTRACT. Pseudoscorpions (*Chthonius ischnocheles* (Hermann) and *C. orthodactylus* (Leach) *sensu strictus*) were collected using a D-Vac over two-years from 60 field margins at Oxford University farm at Wytham, U.K. Old and new grassland margins were subjected to six different treatments involving spraying, non-intervention and four different cutting intensities. Significantly more pseudoscorpions were found in old compared to new margins, suggesting they may be attracted to litter build-up over time. Pseudoscorpion numbers were reduced on treatments subjected to two cuts annually, particularly when a summer cut was included, although this effect was ameliorated when the cuttings were left. However, pseudoscorpions were most numerous on treatments which involved no management because of the increase in leaf litter which may replicate a woodland environment. Adjacent hedges appear to buffer the effects of management: margins with adjacent hedges (rather than ditches or tracks) having more individuals. In contrast to results for other invertebrate groups, sowing wildflower seed did not significantly increase the abundance of pseudoscorpions. The effect of different treatments on pseudoscorpion numbers demonstrates that they are useful indicators of the effects of management practice.

Leaf litter is the ancestral habitat of pseudoscorpions, with deeper litter, such as that in woodlands, providing an ideal stable environment (Jones 1970). Few studies have examined them in grasslands despite some species occurring commonly in this ecosystem. Fewer still have considered the role of habitat management on pseudoscorpions in grassland margins. Thus, stable woodland environments have provided nearly all the ecological and taxonomic work for common pseudoscorpion families, such as the Chthonidae, in Britain

(e.g., Gabbutt & Vachon 1963; Gabbutt 1967; Goddard 1976; Wood & Gabbutt 1978). Particular attention has been paid to the ecology and life history of *Chthonius ischnocheles* (Hermann) and to a lesser extent *Chthonius orthodactylus* (Leach) *sensu strictus*, both of which are widespread species. It is not surprising that there has been little work on grassland pseudoscorpions since only the *Nanolpium* species (Garypoidea, Olpiidae) from Africa are consistently collected from grass, probably because grasslands are too exposed for many other pseudoscorpions (Judson & Heurtault 1996). In the only British reference to grassland pseudoscorpions, Salt et al. (1948) found high densities (19.56 m^{-2}) in agricultural fields in Cambridgeshire, but unfortunately did not report the species' names. Grasslands are a marginal habitat for several British species including *Chthonius ischnocheles* and *C. orthodactylus* (Legg & Jones 1988), probably because deep litter is found in large amounts only under hedges and in man-made piles. Despite this, Rapp (1978)

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compared the distribution of *Microbisum confusum* Hoff. in two contrasting areas of tall grass and mixed prairie. He determined that grazing caused a decline in the number of pseudoscorpions because of adverse changes to moisture and litter depth. Our paper is the first to examine changes in pseudoscorpion numbers within a unique farm scale environment that has been block designed and replicated to test for successional processes over a long period of time. Over the last ten years, the Oxford University farm at Wytham has been used to test the effect of management on a variety of other grassland arthropods such as spiders (Baines et al. 1998), butterflies (Ferber et al. 1996) and the Hemiptera (Smith et al. 1993), producing a better understanding of the habitat requirements of these groups in an agricultural context. We use this field experiment, designed to evaluate the wildlife conservation benefits of a variety of management techniques for arable field margins, to examine the effects of age, management and proximity to mature boundary habitats on pseudoscorpions. Our hypothesis that low intensity management and stable conditions found in hedges will support more individuals is based on a pseudoscorpion's sensitivity to litter depth and mutable habitat structures.

METHODS

Site management.—The surveys took place at the site of an experiment established in 1987 on 60 field margins at Oxford University farm (SP 472 097) at Wytham (Smith et al. 1993; Feber et al. 1996). Old margins ($n = 60$) around the fields existed pre-1987 and are about 1 m wide. In 1988 these old margins were extended 1 m into the field to a total width of 2 m and producing new margins ($n = 60$). In 1990 sterile strips were cultivated between the margin and the crop, allowing access to the margins without trampling. Six management treatments in 50 m strips were randomized in a block design across the 60 margins. Treatment A had no management ($n = 12$); B was cut in spring and autumn and the hay collected ($n = 12$); C was cut in spring and summer and the hay collected ($n = 12$); D was cut in summer only and the hay collected ($n = 12$); E was cut in spring and summer and the hay left ($n = 6$); F was sprayed with herbicide (glyphosate) in the same way as the crop ($n = 6$). Those treatments with a

sample size of 12 (A–D) were subdivided into margins which were sown with wildflower seed in March 1988, and those which were left to colonize without sowing ($n = 6$ in each case). Cutting took place in spring (April), summer (June) and autumn (September) using an Allen scythe and brush cutters. The cuttings were left to dry and the hay was collected or left depending upon the treatment. Glyphosate (Roundup BiactiveTM, Monsanto) was applied to six margins (F) at a rate of 3 liters ha^{-1} at a field volume of 200 liters ha^{-1} using an Oxford precision sprayer. The habitats adjacent to the margins were recorded: ditches ($n = 56$), hedges ($n = 38$), and tracks ($n = 26$).

Sampling.—Pseudoscorpion species (*Chthonius ischnocheles* and *C. orthodactylus*) were collected for two field seasons in 1995 and 1996 using a Dietrick Vacuum suction sampler (D-Vac). During each season, samples were collected in spring (May), summer (July) and autumn (September). Five sucks of 30 seconds were made, each at a 10 m interval along a 50 m margin, and were aggregated to give one sample. The samples were taken separately from old and new margins. Specimens were separated from debris in the laboratory and stored in 70% methanol. No attempt was made to collect silken chambers and this may have underestimated the true number of females of both species and protonymphs of *C. orthodactylus* (Gabbutt 1970; Goddard 1976). D-Vac sampling is biased towards collecting samples from the litter layer. We made no attempt to collect samples from the soil which may have underestimated actual numbers within each margin. Adult specimens were identified using Legg & Jones (1988), and nymphal stages were identified using Gabbutt & Vachon (1963) and unpublished drawings by Mark Judson (Muséum National D'Histoire Naturelle, Paris).

Statistical analysis.—Both species, and the six collections over two years, were aggregated to simplify analysis. The Kolmogorov-Smirnov two sample test indicated that it was not possible to transform the data to normality, therefore we used non-parametric statistics to test for difference. Non-specific Meddis rank means tests were used, blocking by treatments not under investigation and using post hoc analyses to identify ideal rank orders where significant results were obtained (Med-

dis 1984). The level of significance for all the tests was where $P \leq 0.05$.

RESULTS AND DISCUSSION

A total of 247 specimens (*Chthonius ischnocheles*: 57♂, 47♀, 54 tritonymphs, 8 deutonymphs = 166. *C. orthodactylus*: 34♂, 24♀, 21 tritonymphs, 2 deutonymphs = 81) was recorded over the two year period. As a proportion of the total number of invertebrates collected from the field margins during this study ($\sim 6 \times 10^5$, excluding Collembola and Acari), the pseudoscorpion population was less than 0.05%. This highlights the relatively minor role of pseudoscorpions in grassland litter compared with woodland litter and soil, in which pseudoscorpions are at relatively high densities (Goddard 1976; Gabbutt 1967). *Chthonius ischnocheles* were twice as abundant and twice as widely distributed over the field margins compared to *C. orthodactylus*. Overall, pseudoscorpions exploited 43.4% of the available field margin habitat ($n = 120$) but in only 9.6% of samples ($n = 120$) did the two species occur together. The ratio of males to females was slightly biased in favor of males for both *C. ischnocheles* (1.2:1) and *C. orthodactylus* (1.4:1). In both species, tritonymphs contributed substantially to the total numbers (*C. ischnocheles* = 32.5%; *C. orthodactylus* = 25.9); but deutonymphs were rare (*C. ischnocheles* = 4.8% ; *C. orthodactylus* = 2.5). No protonymphs were recorded.

Age of margins.—Significantly more pseudoscorpions were found in old margins compared with new ($H = 9.471$, $P = 0.002$, $df = 1$). This may be a due to litter build-up over time, since deeper litter supports more individuals and suitable prey (Jones 1970). Both Baines et al. (1998) and Frank & Nentwig (1995) recorded more spider species, and more individuals, on older field margins compared to new. Although spiders and pseudoscorpions differ in their habitat requirements, it may be that the longer the field margin has to develop, the more stable and ultimately more suitable the litter environment becomes.

Management.—The timing and the intensity of management had a significant impact on the abundance of pseudoscorpions (see Table 1) found in the field margins ($H = 12.712$, $P = 0.026$, $df = 5$, rank order: A>D,E,B>F>C). No management (A) was associated with higher abundances (Table 1) when compared

Table 1.—Comparison of the effect of treatment on total pseudoscorpion numbers expressed as a rank. Species counts are also given but were not tested separately and should not be compared with the *post hoc* rank scores. The test using a non-specific Meddis rank means test was significant ($P = 0.026$). The *post hoc* ranks range from 1 (the highest) to 4 (the lowest) scores; D, E, B are not significantly different and therefore have the same rank score.

Treat- ment	<i>Chthonius</i> <i>ortho-</i> <i>dactylus</i>	<i>Chthonius</i> <i>ischno-</i> <i>cheles</i>	Combined spp. total	<i>Post</i> <i>hoc</i> rank
A	37	58	95	1
B	4	25	29	2
C	9	10	19	4
D	25	28	53	2
E	4	26	30	2
F	2	19	21	3
Totals	81	166	247	—

with other treatments, probably because it allowed litter build-up, provided cover and a comparatively stable microclimate. Timing and frequency of cutting are critical for other invertebrate groups (e.g., Morris & Rispin 1988) with summer cuts being deleterious to spiders (Baines et al. 1998). When a summer cut is combined with a spring cut and the clippings are collected on both occasions (C), it has a more serious effect on pseudoscorpion numbers (Table 1). Effectively this management treatment produces a grassland sward that is short, with minimal litter development and an unstable microclimate. Rapp (1978) recorded a similar effect under grazing where the abundance of *Microbisum confusum* was determined by the thickness of the litter and available soil moisture. Frequent cutting of grassland creates a high degree of disturbance and structural alteration through removal of standing vegetation (Morris 1979). Plant architecture and floral composition are governed by management (Brown & Gibson 1990) which in turn causes the microclimate within the sward to change (Morris 1968; Morris & Rispin 1988). Dramatic fluctuations in the microclimate, particularly humidity and temperature, will have a negative impact on pseudoscorpions, (Weygoldt 1969; Rapp 1978). *Chthonius ischnocheles* can recover lost water with changes in humidity quickly and will migrate in adverse conditions (Caplin 1974;

Legg & Jones 1988) but probably not over a sustained period with little vegetation cover.

Management treatments B, D and E were similar to each other in terms of the abundance of pseudoscorpions (Table 1), but supported fewer individuals than did A. These results suggest that a single summer cut (D) or two cuts which avoided the summer period (B) have less impact than a spring and summer cut with removal of the vegetation (C). When two cuts close together are necessary, leaving the hay on the margins appears to ameliorate the effects of this intensive regime (E). Ideally, we advocate that, in order to achieve a balance with the habitat requirements of other invertebrate groups, management B, D and E are acceptable compromises, and leaving grass piles on the margin would increase litter availability, but probably encourage weeds (Smith pers. comm.). Our study suggests that pseudoscorpions are sensitive to herbicide applications (F), although this is not as deleterious to pseudoscorpions as a spring and summer cut with removal of vegetation (C) (Table 1). Such spraying generates a deeper litter over a period of months, creating an ideal habitat for pseudoscorpions (Jones 1970) but it is suggested that consequent changes in microclimate may render conditions unsuitable.

Boundary habitats.—The three types of boundary habitat adjacent to the field margins had a significant impact on the numbers of pseudoscorpions found in the field margin ($H = 7.286$, $P = 0.025$, $df = 2$, rank order: $H > D > T$). Margins adjacent to a hedge (H) had more individuals than those adjacent to a ditch (D), but the poorest adjacent habitat was a track (T). Moisture, light and food availability are often relatively stable in hedgerows (Hance et al. 1990), but in field systems which have a high level of disturbance from management (Morris 1979) these must be in a state of flux (although soil moisture may not change significantly: White & Hassall (1994)). The hedge and, to a lesser extent, the ditch could act as a buffer and possible overwintering site and refuge from extremes of management. Tracks are less likely to buffer populations as they are highly disturbed by farm traffic and subject to substantial diurnal variations in temperature.

Wildflower seeded margins.—No significant difference was detected in abundance be-

tween margins sown with a wildflower seed mixture and those left to be colonized naturally ($H = 0.969$, $P = 0.674$, $df = 1$). As most pseudoscorpions live within the litter, their numbers are not as directly affected by the diversity of vegetation in field margins, as are the numbers of spiders, which are dependent on vegetation structural complexity and diversity (White & Hassall 1994; Baines et al. 1998). However, there are benefits of sowing to other groups of invertebrates, e.g., *Maniola jurtina* L. (Lepidoptera) (Feber et al. 1996).

Conclusions.—Although pseudoscorpions are not an abundant group in grasslands, they are good indicators of mutable habitat structures. The differences detected among different management regimes, age structures and adjacent habitats supports our hypothesis that the management of field margins for arthropods should be consistent over time and of low intensity creating a suitable litter environment. Hedges clearly buffer the populations of pseudoscorpions within field margins and should be conserved. Although sowing field margins with wildflowers had no detectable effect, this practice benefits other invertebrate groups and should be encouraged.

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COMPARATIVE ANALYSES OF EPIGEIC SPIDER ASSEMBLAGES IN NORTHERN HUNGARIAN WINTER WHEAT FIELDS AND THEIR ADJACENT MARGINS

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ABSTRACT. Pitfall trapping was carried out in northern Hungarian winter wheat fields and their adjacent margins during the growing seasons of three consecutive years, 1992–1994. The dominant species of both habitats was the wolf spider *Pardosa agrestis* (Westring). A total of 8403 adult individuals of 19 families of 149 spider species was identified: 118 species from the winter wheat and 118 from the margins with fewer traps. The efficiency of detecting species by trapping was 90%, according to the Baule-Mitscherlich extrapolation model. Provided that the sampling effort is the same in both habitats, traps in the margin may catch higher number of individuals and species, than traps located within the field. Calculations, however, indicate that the field, with an area more than a hundred times larger than that of the margins, has a higher total number of species. Although the spider species spectrum of the field and of the margin had a considerable overlap, the Renkonen similarity index indicates that the spider fauna of the two types of habitats were different. Spider assemblages of the margins were more diverse (Rényi diversity), than those of the fields. The species richness of epigeic spiders in our Hungarian winter wheat fields was high, and it was increased by the presence of margins. Thus, for the purposes of the protection of our fauna and promotion of integrated pest management, establishment and maintenance of margins is strongly desirable.

Recent development of the Hungarian agriculture shows an increased attention to land use in general. Re-evaluation of former land use (share of field crops, reforestation of areas that are not suitable and economical for crop production), implementation of the basic principles of the “National Strategy for Conservation of Biodiversity” (Hungarian Academy of Sciences) reflects the importance of agrarian biotopes. Parallel to this, the present development of plant protection is focusing on the potential of natural enemies in integrated pest management (IPM), which involves maintaining their habitats and applying management practices that have minimal adverse effect.

Winter wheat and corn are the two most important crops grown in Hungary. Winter wheat covers about 25% of the arable land. Only a few data sets concerning the spider assemblages of arable lands in Hungary are available. Balogh & Loksa (1956), Samu et al. (1996) and Németh (1996) have examined the spider community in alfalfa fields. According to a recent bibliography of Hungarian arachnological studies (Szinetér & Samu 1995), the present research is the first to study

the spider fauna of winter wheat in Hungary. Our preliminary surveys in winter wheat showed that spiders are among the dominant epigeic predators in winter wheat in Hungary (Kiss et al. 1993, 1994, 1998). Thus our study aimed to analyze the spider assemblages of winter wheat fields and their adjacent margins with respect to biotic diversity and the development of IPM.

METHODS

Description of study area and traps.—The study area was located in northern Hungary in the vicinity of the village Kartal (latitude 47°40'). Three winter wheat fields, Kartal 1 (K1), Kartal 2 (K2) and Józsefmajor (JM) and their adjacent margins less than 6 km apart were surveyed by pitfall traps in three consecutive years. Diameter of the pitfall traps was 10 cm. A 2% formalin solution with a drop of detergent was placed in traps as a preservative. The traps were run continuously and were emptied weekly, except in winter (in K2) when they were emptied monthly. Hereafter when we refer to a trap row we mean 5 traps placed in a row parallel to the closest field margin.

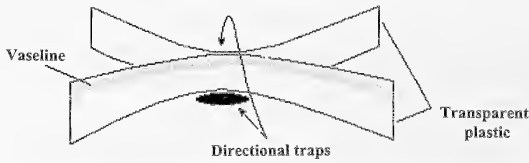


Figure 1.—A pair of directional pitfall traps in Józsefmajor field (JM) (1994).

Annual precipitation in the region is about 600–650 mm. Direction of the prevailing winds is highly variable. The topsoil is Luvic chernozem, developed on loess, mixed with weathered local andesitic material, that explains the more clayey texture than the loess origin would suggest. During the dry season in summer the topsoil in the fields opens 1–2 cm wide deep cracks. Field margins were abandoned, uncultivated and untreated strips at the edge of the fields, covered by an herbaceous undergrowth and containing a few separate trees (*Robinia pseudoacacia*) and shrubs (*Robinia pseudoacacia*, *Sambucus nigra*, *Rubus caesius*, *Prunus spinosa*). Coenological details are given in Kiss et al. (1997).

The K1 field measured 131 hectares. The margin was 2–3 m wide. Fifteen pitfall traps were operated in three parallel rows from late April until harvest in early July 1992. One row of traps was in the margin, parallel to the ecotone (5 m apart from each other), and two more were positioned into the field at increments of 30 and 250 m from the margin.

The area of the K2 field was 250 hectares. The margin was 2–3 m wide. Twenty pitfall traps were operated in four rows parallel to the ecotone from early November 1992 throughout winter until harvest in early July 1993. Five traps were placed in the margin (5 m apart from each other), and the other trap rows were in the field at increments of 20, 50 and 250 m from the margin.

The area of the JM field was 61 hectares and the margin was 4–5 m wide. Twenty pitfall traps were operated in four rows parallel to the ecotone from mid-March until harvest in mid-July 1994. Five traps were placed in the margin (10 m apart from each other) and the other trap lines were placed in the field at increments of 20, 50 and 250 m from the margin. Three pairs of directional pitfall traps, 20 m apart were placed in the JM field, 1 m from the margin (Fig. 1). A pair of directional traps

consisted of two pitfall traps, separated by two transparent U-shaped plastic plates. The plates were 1 meter long, 30 cm tall and were sunk into the ground to a depth of 10 cm. The upper edge of the plates was smeared with a thick layer of vaseline to inhibit climbing by arthropods. Traps facing the margin are called 'Dir. M', whereas traps facing the field are called 'Dir. F'. Directional traps enabled us to determine whether the spider assemblage of the immediate area of the margin (1 meter within the field) is similar to that of the margin or of the field.

Data analyses.—Since immature spiders are difficult to identify, only adults were taken into account in the analyses of extrapolation, similarity and diversity models, and all were identified to species level.

Extrapolation: The potential number of species caught in traps was estimated with the Baule-Mitscherlich function (Sváb 1981; Samu & Lövei 1995). The equation is:

$$y = T(1 - e^{-ax})^b$$

where T means the potential number of species (saturation level), a and b are parameters, x (independent variable) is the cumulative number of individuals, and y (dependent variable) equals the cumulative number of species. Trapping results were randomly sorted and successively simulated an increase in sampling effort. Saturation level of the function best fitting the points was calculated using an iterative least squares grid searching method. Randomization of the trapping data and calculation of the saturation level (T) was repeated 50 times and the means were used in each case as the potential number of species. Potential number of species was calculated for both habitat types separately (field or margin), and combined (field + margin).

Similarity: Similarity of the spider assemblages of different trap rows was calculated with the Renkonen index (Renkonen 1938). The equation is:

$$R = \sum \min(p_i, q_i)$$

where p_i and q_i mean the relative frequency of species number i in habitats p and q. Since operating with relative frequencies, the captures are re-scaled between 0 and 1. So the Renkonen index enables us to compare results of different sampling efforts. In order to make the comparison of spider assemblages of the

Table 1.—Number of spider species and adult individuals captured in pitfall traps in three Hungarian winter wheat fields and in their adjacent margins (1992–94). Numbers in brackets imply that the results of directional pitfall traps has been added. (K1 = Kartal field 1; K2 = Kartal field 2; JM = Józsefmajor field. Distance of field traps from the margin is indicated.)

Field (year)	Margin	20(30) m	50 m	250 m	Wheat total	Total
Number of species						
K1 (1992)	57	38		31	54	77
K2 (1992–93)	72	34	35	37	55	91
JM (1994)	77	56	57	44	83 (97)	103 (111)
Total	118				107 (118)	145 (149)
Number of adult individuals						
K1 (1992)	1073	738		764	1502	2575
K2 (1992–93)	706	245	286	378	909	1615
JM (1994)	882	882	819	719	2420 (3331)	3302 (4213)
Total	2661				4831 (5742)	7492 (8403)

three different fields more reliable, autumn and winter catches in K2 were not included in this analysis. The similarities were also illustrated by a dendrogram, which shows the results of a hierarchical cluster-analysis using single linkage and the Renkonen index as distance measure data.

Diversity: The Rényi-function (Tóthmérész 1993) was used to characterize species diversity of different trap rows. Rényi-diversity:

$$H_{\alpha} = (\ln \sum (N_i/N_T)^{\alpha}) / (1 - \alpha)$$

where $0 < \alpha, \alpha \neq 1$, N_i means the number of individuals of the species number i , T means the total number of species, N_T means the total number of individuals, and α is a scale parameter. Where the scale parameter is low, the function is more sensitive to rare species, whereas high values of the scale parameter suggests that the function is more sensitive to the dominant species. If $\alpha \rightarrow 1$, then $H_{\alpha} \rightarrow H_S$ (H_S : Shannon diversity). If $\alpha = 0$, then $H_{\alpha} = \ln T$. Species richness was expressed by the Margalef-index (Margalef 1958). The equation is:

$$d = (S - 1) / \ln N$$

where S means the number of species, N means the number of individuals.

RESULTS

The dominant spider species in our Hungarian winter wheat fields was *Pardosa agrestis* (Westring) (43% of wheat total), followed by *Oedothorax apicatus* (Blackwall) (16%), *Meioneta rurestris* (C.L. Koch) (11%), *Xysticus kochi* Thorell (3%), *Trichoncoides pisca-*

tor (Simon) (3%) and *Zelotes mundus* (Kulczynski) (3%). The dominant species of field margin spiders was also *Pardosa agrestis* (17% of margin total), followed by *Pardosa prativaga* (L. Koch) (7%), *Zelotes pedestris* (C.L. Koch) (6%), *Aulonia albimana* (Walckenaer) (5%), *Hahnia nava* (Blackwall) (5%) and *Xysticus kochi* Thorell (4%).

A total of 8403 adult individuals of 149 spider species was identified. From the winter wheat, 118 species were collected and similarly (with fewer traps), 118 species were collected from the margin. There were 87 species (58.4% of total) which occurred in both habitats. Margin trap rows collected larger number of individuals and species than field trap rows in the same field. Directional traps at JM collected 911 adults of 69 species. This increased the number of species in wheat total (K1 + K2 + JM) by 11 species. The directional trapping added only 4 species to the total (Table 1).

According to the Baule-Mitscherlich extrapolation model, the potential number of species caught with pitfall traps in these fields given the trap numbers and configuration was 164 ($r^2 = 0.981$) for the total area (field + margin), 135 ($r^2 = 0.979$) for the wheat, and 130 ($r^2 = 0.980$) species for the margin. The model suggests that 116 species is predicted to occur in both habitats. This means a 70.7% potential overlap between the species spectrum of field and margin, compared to the observed overlap of 58.4%.

In all the three fields, species composition of trap rows of the same field were highly

Table 2.—Renkonen similarity indices comparing adult ground spider assemblages captured in pitfall traps positioned in three Hungarian winter wheat fields and in their adjacent margins (1992–94). Indices were computed from relative frequency of species. (K1 = Kartal field 1; K2 = Kartal field 2; JM = Józsefmajor field. Distance of field traps from the margin is indicated. Dir. M./Dir. F. = directional traps facing the margin/field.)

	K1 Mar- gin	K1 30 m	K1 250 m	K2 Mar- gin	K2 20 m	K2 50 m	K2 250 m	JM Mar- gin	JM Dir. M.	JM Dir. F.	JM 20 m	JM 50 m
K1 30 m	0.50											
K1 250 m	0.45	0.83										
K2 Margin	0.32	0.18	0.16									
K2 20 m	0.40	0.56	0.51	0.22								
K2 50 m	0.38	0.56	0.50	0.19	0.83							
K2 250 m	0.41	0.58	0.52	0.21	0.78	0.80						
JM Margin	0.40	0.25	0.23	0.44	0.32	0.27	0.30					
JM Dir. M.	0.53	0.58	0.57	0.29	0.65	0.59	0.65	0.43				
JM Dir. F.	0.49	0.52	0.50	0.27	0.55	0.49	0.55	0.46	0.79			
JM 20 m	0.44	0.62	0.59	0.20	0.66	0.60	0.65	0.34	0.79	0.79		
JM 50 m	0.43	0.60	0.57	0.18	0.67	0.61	0.69	0.31	0.75	0.75	0.89	
JM 250 m	0.42	0.57	0.56	0.18	0.54	0.47	0.55	0.30	0.72	0.78	0.80	0.79

similar ($R = 0.72\text{--}0.89$) (Table 2; Fig. 2). Species composition of margins differed more either from that of the other margins ($R = 0.32\text{--}0.44$) or from that of the field trap rows ($R = 0.16\text{--}0.53$). The lowest field-field similarity ($R = 0.47$) was higher than the highest margin-margin similarity ($R = 0.44$). Directional trap catches, oriented to capture spiders moving across the edge were highly similar to each other ($R = 0.79$) and to the field catches ($R = 0.72\text{--}0.79$).

The Rényi-diversity of margin trap rows were higher than those of the field trap rows of the same field, regardless of concentrating on rare (when scale parameter is low) or dominant (when scale parameter is high) species (Fig. 3). Species richness of the total capture is characterized by a Margalef-index of $d = 16.4$, whereas the index for wheat is $d = 13.5$, and $d = 14.8$ for margin.

DISCUSSION

Field margin seems to be a more dense and rich habitat than field, since traps in the margins usually catch higher number of individuals and species, than traps located within the fields (Kromp & Steinberger 1992; Al Hussein & Lübke-Al Hussein 1995; Samu et al. 1996). This experience, however, does not necessarily means that the total number of species is higher in the margins because the total area of the fields is much larger than that

of the margins. Overlap between the number of spider species in the margin vs. field may be as high as 70%. The proportion of species occurring in both habitats is influenced by the sampling effort, so comparability is more reliable with the Renkonen index than with the species list overlap. Similarity between margin and field was found $R = 0.18$ (Kromp & Steinberger 1992), $R = 0.21\text{--}0.53$ (Al Hussein & Lübke-Al Hussein 1995), and $R = 0.62$ (Janssens & De Clercq 1986), whereas in-field similarity was $R = 0.82\text{--}0.95$ (Al Hussein & Lübke-Al Hussein 1995). These data and our findings suggest that margin-field or margin-margin similarity usually remains under 0.5, while field-field similarity values in most cases exceed this level. This is explained by that the fields are strongly and repeatedly disturbed every year by tillage, harvest, pesticide application and other field works, while occasional disturbance in the margins (mowing, pesticide drifting) does not destroy the habitat basically. As a consequence, pioneer spider species, such as *Oedothorax spp.*, *Meioneta spp.*, *Erigone spp.*, *Pardosa spp.*, *Trochosa spp.*, *Pachygnatha spp.* dominate the European arable fields, resulting in a relative uniformity. Most of these pioneer species are frequent in the margins as well, but spider assemblages of the margins are more diverse than those of the fields (Kromp & Steinberger

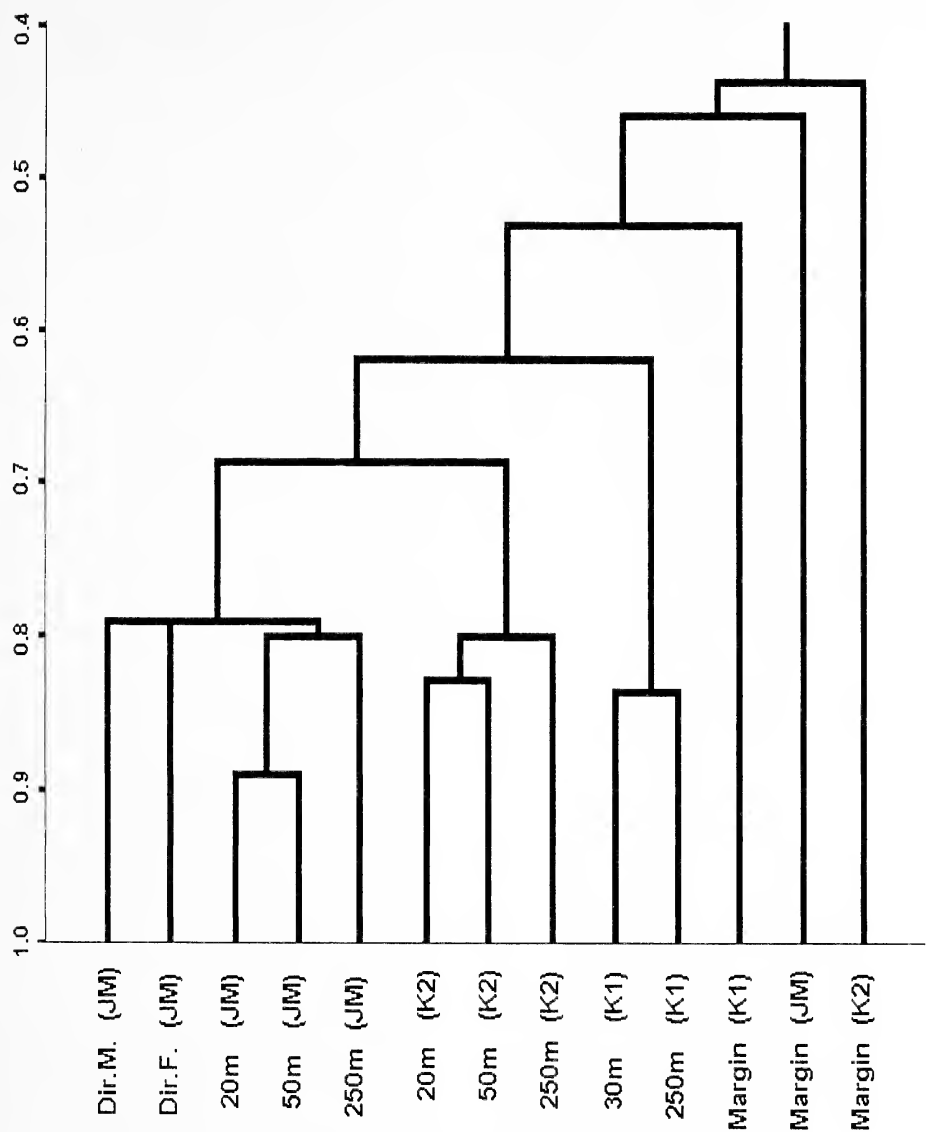


Figure 2.—Similarity of the spider assemblages of three Hungarian winter wheat fields and of their adjacent margins. The dendrogram illustrates the result of a hierarchical cluster analysis using single linkage and the Renkonen index, calculated from relative frequency data of species. (K1 = Kartal field 1; K2 = Kartal field 2; JM = Józsefmajor field. Distance of field traps from the margin is indicated. Dir. M./Dir. F. = directional traps facing the margin/field.)

1992; Al Hussein & Lübke-Al Hussein 1995; Samu et al. 1996). Ground spider species richness in these northern Hungarian winter wheat fields and their adjacent margins were higher than those found in other such surveys in European agricultural areas (Table 3). For the explanation of this phenomenon further investigations are needed.

According to the IOBC Technical Guidelines for arable crops (Boller et al. 1997) eco-

logical compensation areas (reservoirs of pest antagonists, like flowering field margins, groups of trees, ponds, haystacks) have to cover at least 5% of the entire farm surface excluding forests. It means that calculating with a 5m wide field margin, the average field size should not exceed 1–2 ha. As a result of the large scale farming, that was characteristic of Hungary until 1989 (Kiss et al. 1997) we estimate that field margins cover around 1%

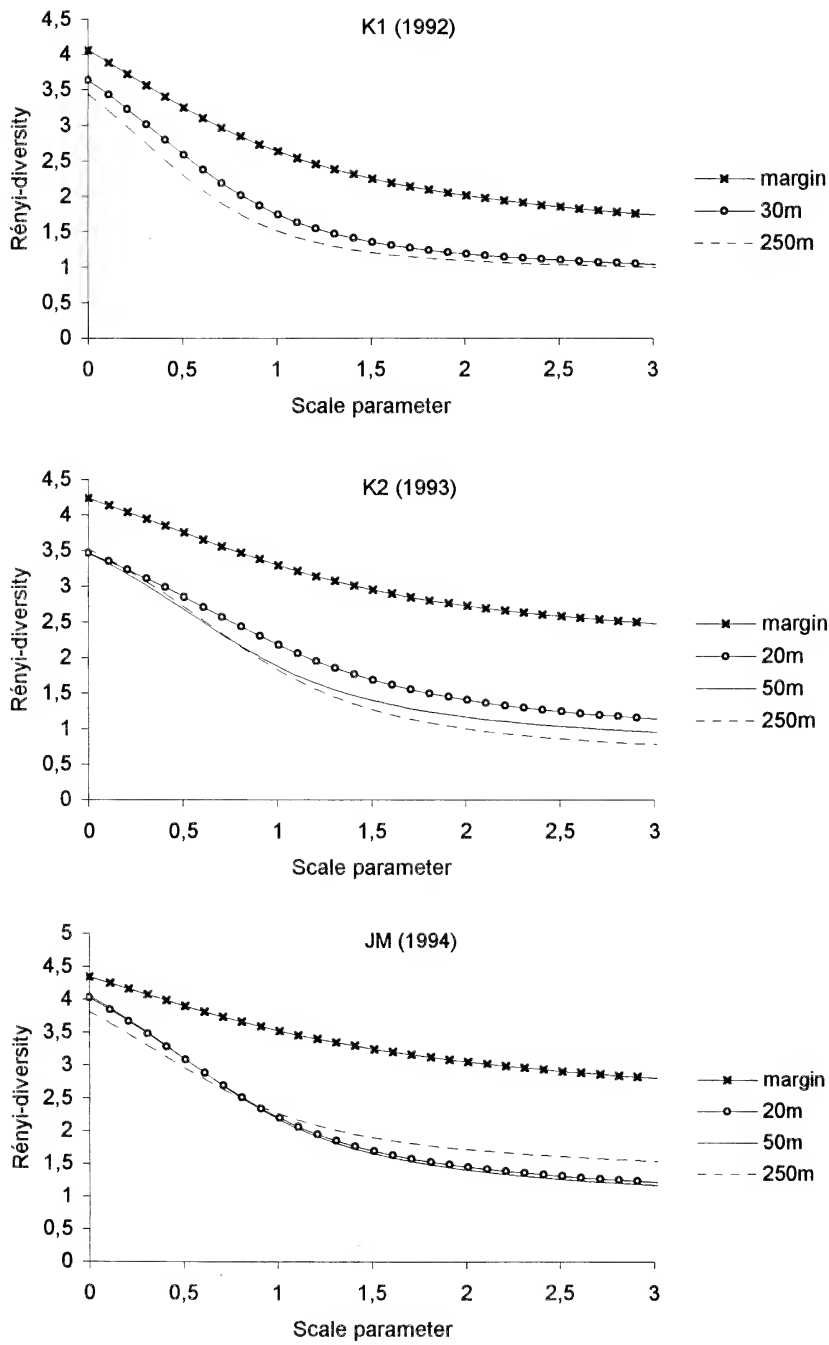


Figure. 3.—Rényi-diversity (H_α) in three Hungarian winter wheat fields and in their adjacent margins, calculated from relative frequency data of spider species. Where the scale parameter (α) is low, the function is sensitive to the rare species, whereas increasing the scale parameter results in a higher sensitivity to the dominant species. If $\alpha \rightarrow 1$, then $H_\alpha \rightarrow H_S$ (H_S : Shannon diversity). If $\alpha = 0$, then $H_\alpha = \ln T$ (T = number of species). (K1 = Kartal field 1; K2 = Kartal field 2; JM = Józsefmajor field. Distance of field traps from the margin is indicated.)

Table 3.—Spider species richness in different European pitfall trap studies, according to the Margalef-index (d), computed from the number of individuals (n) and species (S).

Habitat	n	S	d	Reference
Total catch	8403	149	16.4	Present study (Tóth & Kiss 1999)
Winter wheat	5742	118	13.5	
Margin	2661	118	14.8	
Winter wheat and sugar beet	101,213	122	10.5	Janssens & De Clercq (1986)
Maize	2018	19	2.4	Alderweireldt & Desender (1990)
Winter wheat, peas and maize	1235	47	6.5	Gajdos (1992)
Winter wheat	4460	80	9.4	Kromp & Steinberger (1992)
Winter wheat	5069	41	4.7	Topping & Sunderland (1992)
Potato and margin	5145	75	8.7	Steinberger & Kromp (1993)
Winter wheat, winter barley and margin	9510	82	8.8	Al Hussein & Lübke-Al Hussein (1995)

of our arable lands. Owing to the rich epigeic spider fauna, Hungarian agroecosystems have a considerable potential to enhance natural enemy populations and their diversity by increasing the number, width and quality of field margins.

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THE EFFECTS OF DIFFERENT RATES OF THE HERBICIDE GLYPHOSATE ON SPIDERS IN ARABLE FIELD MARGINS

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ABSTRACT. Field margins are susceptible to agro-chemical spray drift, and the effects of herbicide on spiders in semi-natural habitats have been little studied. In this experiment, an arable field margin was sprayed with three rates of glyphosate (90 g active ingredient/hectare (a.i./ha), 180 g a.i./ha & 360 g a.i./ha) and control plots left unsprayed. Spiders were sampled monthly (June–October) using a converted garden-vac and adult spiders were identified to species. A total of 23,393 spiders was sampled with the web-spinners representing more than 90% of the individuals. The effects of glyphosate application on the abundance of wandering and web-spinning prey-capture guilds, and the two most abundant species (*Gonatium rubens* and *Lepthyphantes tenuis*) were analyzed using ANOVA F tests. The highest rate of glyphosate consistently reduced the total number of spiders, the numbers of web-spinners, *G. rubens* and *L. tenuis*, but not numbers of wandering spiders. Changes in vegetation structure and microclimate caused by the glyphosate are implicated in the reduction of numbers of spiders in plots receiving the highest rate of glyphosate. We conclude that glyphosate drift at rates of more than 360 g a.i./ha (active ingredients per hectare) into arable field margins could result in significant losses of important arthropod predators in farmland and a reduction in spider biodiversity in agroecosystems.

In the United Kingdom, arable field margins commonly comprise a boundary (hedge, fence, wall, or ditch) and a grass-dominated boundary strip, and these constituent parts have been shown to be beneficial in enhancing flora, mammals, game birds and insects on arable farmland (e.g., Boatman 1994). Arable field margins are important as overwintering sites (Bayram & Luff 1993), permanent habitats (Alderweireldt 1994a) and refuges for recovery (Thomas et al. 1991) for spiders in the agroecosystem. Not only do arable field margins increase the opportunity for enhancing spiders as predators (Alderweireldt 1994a), but they are able to increase spider-biodiversity within biologically-impoverished arable land (Duelli et al. 1990).

Field margins are susceptible to direct herbicide applications (Boatman 1989) and also to spray drift by the virtue of their proximity to high-input cropped areas. Glyphosate is a commonly used herbicide and with the development of herbicide resistant crops, the use of non-selective herbicides like glyphosate is

likely to increase (Mueller & Womac 1997). Research into the optimum width of buffer zones for reducing spray drift into sensitive areas has recommended margins in the order of 6 m wide for reduction of the most toxic effects of various pesticides (Marrs et al. 1992; de Snoo 1997).

Although the impact of insecticides on spider behavior (Samu & Vollrath 1992) and mortality (Everts et al. 1989) has been studied, the effects of herbicide contamination on spiders remain little-researched (Raatikainen & Huhta 1968; Asteraki et al. 1992). Spiders are sensitive to changes in vegetation structure, where a highly variable structure provides web-spinners with increased web-site opportunities. Availability of structural support for webs and a suitable micro-climate (ameliorated fluctuations in humidity and temperature) are the most important factors in web site selection (Samu et al. 1996). The intrinsic action of herbicide on plants alters both the vegetation structure and therefore microclimate conditions, and so it is likely that changes in spi-

der fauna would occur when a habitat is exposed to a herbicide application. Here, we subjected an arable field margin to a herbicide application to establish whether relative spider population, prey-capture guild and number of individuals of abundant species were affected.

METHODS

Site.—A well established arable field margin was selected on the Allerton Research and Educational Trust's Loddington Estate in Leicestershire, UK. The field margin was dominated by couch grass (*Elymus repens* (L.)) and false oat grass (*Arrhenatherum elatius* (L.)) and lay adjacent to a dense uncut hawthorn (*Crataegus monogyna* Jacq.) and blackthorn (*Prunus spinosa* L.) hedge. The field margin was east-south-east facing on slightly stoney clay soils from the Hanslope Series and the field was sown to winter barley (cultivar: Fighter).

Treatments.—Eight replicates of four treatments (90 g active ingredient/hectare (a.i./ha), 180 g a.i./ha & 360 g a.i./ha glyphosate and control) were randomly applied to adjacent field margin plots, which measured 12 m \times 1 m. The glyphosate (Roundup BiactiveTM, Monsanto) was applied to the plots at a volume rate of 200 liters/ha and a pressure of 25 bars using an Oxford Precision sprayer on 30 May 1997.

Sampling.—Spiders were sampled using a modified garden-vac (g-vac) (Ryobi RSV3100E). As a relatively new arthropod sampling device, the g-vac has received critical attention. Its sampling efficiency has been reviewed and the machine used in this experiment has been considered to be an effective method of sampling spiders (Samu et al. 1997). The g-vac samples comprised 10 sub-samples of 30 second 'sucks' at 1 m intervals along each experimental plot. This approximated to a total sampling area per plot of 0.13 m². The invertebrate samples were cooled immediately and then extracted with an aspirator into 70% alcohol before being identified. All adult spiders were identified to species, whilst immatures were included in total number of spiders.

Spiders were sampled prior to the herbicide application to confirm that plots did not support different abundances of spiders. Spiders were then sampled two weeks post-herbicide application and monthly thereafter. Spiders were sampled from June to October inclusive.

Statistical analysis.—Total spider abundance data and prey-capturing guild data were $\log(x + 1)$ transformed while spider species abundance data were square-root ($x + 0.5$) transformed. Two-way univariate repeated measures ANOVAs were used to test for differences in mean number of spiders between treatments because the samples of spiders through the season could not be considered to be independent of each other (Von Ende 1993). Where an interaction between treatment and date existed, indicating that the effect of treatment differed between dates, a one-way univariate ANOVA was used to test for differences in mean number of spiders between treatments in each month. Planned comparisons were used to test for differences implicit in the experimental design: we used Least Significant Difference (LSD) tests to determine differences between means (Sokal & Rohlf 1995).

RESULTS

A total of 23,393 spiders from 11 families and 67 species was recorded and the dominant family was the Linyphiidae. Specimens have been deposited at the Liverpool Museum, UK.

Pre-treatment.—Spider abundance did not differ between plots prior to treatment application (ANOVA $F_{(3, 28)} = 1.31$; $P = 0.2901$). We therefore considered the plots to be similar in spider fauna composition and proceeded with analysis.

Total spider abundance.—Two-way repeated measures ANOVA indicated that there was a significant date \times treatment interaction ($F_{(15, 140)} = 2.69$; $P < 0.0013$), so we analyzed data from individual months. Total abundance of spiders was only significantly different between treatments in September (one-way ANOVA $F_{(3, 28)} = 4.01$; $P < 0.0171$), where significantly fewer spiders were found in the 360 g a.i./ha treatment than in all other treatments (Table 1).

Prey-capture guilds.—Web-spinning adult spiders from the Tetragnathidae, Theridiidae and Linyphiidae and wandering adult spiders from the Thomisidae, Clubionidae, Pisauridae, Zoridae, Oonopidae and Lycosidae were grouped to investigate the treatment effects on these two prey-capture guilds. Table 2 shows the mean number of individuals from the families in the two guilds in each of the treatments. Web-spinning spiders were dominated

Table 1.—Mean total number of spiders in treatments and LSD *P* values for differences between means in all treatments and 360 g active ingredient/hectare (a.i./ha).

	Control	90 g a.i./ha	180 g a.i./ha	360 g a.i./ha
mean	220.50	205.13	209.38	152.13
<i>P</i>	<0.0037	<0.0174	<0.0136	—

by the Linyphiidae and were more abundant than wandering spiders, where they represented more than 90% of individuals in these two guilds. Wandering spiders were not found to differ between treatments (repeated measures ANOVA $F_{(3, 28)} = 0.67$; $P < 0.5779$).

Two-way repeated measures ANOVA indicated that there was a significant treatment by date interaction ($F_{(12, 112)} = 2.61$; $P < 0.0042$) for web-spinners, so we analyzed data from individual months. The number of web-spinners was significantly different among treatments in August, September and October, where more spiders were found in the control plots than in the 360 g a.i./ha in September and October only (Table 3).

Species data.—Only species which occurred in sufficient numbers (mean number individuals > 1.5 in each month) were analyzed individually. Only two linyphiid species fulfilled this criterion and showed significantly different mean abundances among treatments.

Gonatum rubens (Blackwall 1833) showed different abundances in different treatments (repeated measures ANOVA $F_{(3, 28)} = 4.41$; $P < 0.0116$) in months August to October, where the control and 90 g a.i./ha plots had

significantly more individuals (LSD $P < 0.0043$; LSD $P < 0.0072$ for control and 90 g a.i./ha respectively) than the 360 g a.i./ha treatment.

Lepthyphantes tenuis (Blackwall 1852) showed different abundances in different treatments in September and October (repeated measures ANOVA $F_{(3, 28)} = 7.63$; $P < 0.0007$), where each of the other treatments had significantly more individuals than the 360 g a.i./ha treatment (Table 4).

DISCUSSION

General effect of treatment.—Applications of glyphosate at 360 g a.i./ha significantly reduced the abundance of total spiders, web-spinners, *Gonatum rubens* and *Lepthyphantes tenuis*, but not of wandering spiders. The lower rates of herbicide had little or no effect on the abundance of spiders per se; however, this study does not take into effect possible changes in wandering and mating.

The initial effects of the herbicide on the total number of spiders and prey-capture guilds were insignificant, but became more profound as the season progressed. Therefore, it is assumed that spiders are not affected directly by glyphosate (which is generally non-toxic to animals), but indirectly by modifications of other factors, such as habitat, prey availability and microclimatic conditions. The time taken for the herbicide to act on vegetation and change the habitat sufficiently for spiders to exert preferences clearly takes months rather than weeks. Where such effects are widespread, numbers of spiders may be low in the following spring, which is a time when spiders are a determining factor in aphid population dynamics in wheat crops (Cocquempot & Chambon 1990). Thus, our single season study indicates that the longer term effects of herbicide on spiders as biocontrol agents and spider species diversity in agroecosystems are of concern.

Wandering spiders.—The highest rate of herbicide did not significantly reduce the

Table 2.—Mean number of individuals in each family from treatments (June to October). a.i./ha = active ingredient/hectare.

	Control	90 g a.i./ha	180 g a.i./ha	360 g a.i./ha
Wandering spiders				
Thomisidae	—	—	0.4	0.3
Clubionidae	0.4	0.4	0.3	0.4
Pisauridae	—	0.3	—	—
Zoridae	—	0.1	0.1	0.1
Oonopidae	—	—	0.1	—
Lycosidae	2.6	2.4	1.8	4.3
Web spinners				
Tetragnathidae	0.8	0.6	0.8	1.3
Theridiidae	6.8	6.3	10.9	7.3
Linyphiidae	29.2	27.3	32.7	24.1

Table 3.—Comparison of mean number of web-spinners between different treatments & LSD *P* values for differences between means in all treatments and 360 g active ingredient/hectare (a.i./ha).

Treatment	August		September		October	
	mean	<i>P</i>	mean	<i>P</i>	mean	<i>P</i>
control	10.00	ns	28.0	<0.0007	85.25	<0.0061
90 g a.i./ha	8.25	ns	24.75	<0.0059	82.13	<0.0159
180 g a.i./ha	19.25	<0.0226	29.86	<0.0004	82.50	<0.0230
360 g a.i./ha	7.25	—	16.38	—	66.50	—

number of wandering spiders. Wandering spiders generally contain few examples of stenophages (Nentwig 1986) and they may be more adept at finding suitable food items in disturbed habitats due to their prey-capture strategy (Young & Edwards 1990). Thus, a combination of feeding strategy and an available diverse prey source may not have sufficiently deterred the wandering spiders from using the herbicide treated plots.

Vegetation structure can influence not only wandering spider prey recognition (Rovner 1980) but also mate detection (Uetz & Stratton 1982). The indirect effects of herbicide on the ability of spiders to detect mates was not recorded, and we suggest that long-term experiments should concentrate on mating success and feeding ability to investigate any correlations with herbicide use.

Web-spinners.—The action of herbicide on vegetation results in sparse cover and reduced vegetation height (Raatikainen & Huhta 1968) as plants lose their vigor. Web-spinning spiders rely on vegetation structure to provide both web-attachment sites and appropriate humidity (Greenstone 1984; Young & Edwards 1990; White & Hassall 1994). Unlike wandering spiders, web-spinning linyphiids tend

to have preferences for specific prey type (Alderweireldt 1994b). Many web-spinning spiders, therefore, may not utilize sub-standard habitat with a poor prey availability, since they invest energy in web-building (Uetz 1991). The web-spinners in this study represented the dominant prey-capture guild and indicated that higher levels of herbicide resulted in unfavorable habitat. Such losses of important farmland spiders from herbicide misapplications could be significant in terms of conservation of spiders in agroecosystems and in enhancing spiders as predators.

Gonatum rubens: This linyphiid is a litter species (McFerran et al. 1994) and it showed a preference away from heavily sprayed plots. Although autecological literature about *G. rubens* is sparse, as a web-spinning spider it has similar habitat requirements as those outlined above. It must be concluded that all, or a combination of, abundance of web-building sites, availability of prey and level of humidity were sub-standard.

Lepthyphantes tenuis: The most abundant spider in the British agroecosystem is *L. tenuis* (Topping & Lovei 1997). This linyphiid builds webs at 10 cm above the ground and is completely dependent upon web-building for prey (Alderweireldt 1994b). As vegetation height is reduced under exposure to herbicide (Raatikainen & Huhta 1968), the ideal web-building height for *L. tenuis* may become displaced to a height with reduced humidity. Aphids form a large part of the diet of *L. tenuis* (Alderweireldt 1994b) and the spider can reduce the aphid (*Rhopalosiphum padi* L.) population on wheat plants by 34% (Mansour & Heimbach 1993). Thus, *Lepthyphantes tenuis* is an important predator in farmland and reductions caused by herbicide applications should be considered against the benefits of biocontrol.

Table 4.—Comparison of mean number of *Lepthyphantes tenuis* between different treatments & LSD *P* values for differences between means in all treatments and 360 g active ingredient/hectare (a.i./ha).

Treatment	September & October	
	mean	<i>P</i>
control	34.38	<0.0002
90 g a.i./ha	34.19	<0.0005
180 g a.i./ha	31.75	<0.0072
360 g a.i./ha	24.38	—

Conclusions.—Herbicide applications at higher rates reduce the abundance of important predators. Field margins, which are valued as refuges for farmland spiders during winter and periods of disturbance, are susceptible to herbicide spray drift and may suffer losses in spider fauna. Reduced herbicide use in and near field margins is suggested here and elsewhere (Young & Edwards 1990) as a way of enhancing spider populations in agroecosystems not only for biocontrol but also for conservation of spider biodiversity.

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A FAUNISTIC AND ZOOGEOGRAPHICAL REVIEW OF THE SPIDERS (ARANEAE) OF THE BALKAN PENINSULA

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ABSTRACT. The Balkan Peninsula is home to 1409 species, included in 337 genera and 47 families. This number was established after a critical review of the existing literature and taxonomic revision of some available collections containing spider material from this region. The highest number of species is recorded for the territories of Bulgaria (775), Greece (642), Croatia (615) and Serbia (508). This biodiversity depends not only on the size of the regions, but also on the degree of exploration by researchers. The territories of Albania, Turkey, Montenegro and Bosnia are less well investigated. According to their current distribution, the established 1409 species can be classified into 24 zoogeographical categories, grouped into four complexes (widely distributed, European, Balkan endemics, and Mediterranean). The largest number of species belongs to the widely distributed complex, but the most characteristic are the Balkan endemics. Their established number (379 species) is high and reflects the local character of the fauna. This phenomenon can be attributed to the relative isolation of the mountains compared with the lowlands, in the context of paleo-environmental changes since Pliocene. Their high percentage (26.9%) suggests an important process of autochthonous speciation. Thus, the Balkan Peninsula can be considered as a main center of speciation for the European araneofauna.

The spider fauna of the Balkan Peninsula is comparatively well-studied due to the efforts of many araneologists from different countries; but the first large, significant work concerning the spiders of all territories of the region came from Drensky (1936). He reported 1066 species from 35 families which constituted a review of all literature available at that time. Some years later Hadjissarantos (1940) compiled all faunistic data about the spiders of continental Greece. Nikolic & Polenec (1981) combined the data concerning Yugoslavian spiders and reported 1022 species from this country. More recent publications list the fauna of Bulgaria, Greece, Serbia, Macedonia, Montenegro and part of Turkey (Brignoli 1968, 1971, 1972, 1974a, b, 1976, 1977, 1979, 1984, 1986; Deeleman 1976, 1978, 1988, 1993; Deltchev 1979a, b, 1983a, b, 1985, 1988, 1990, 1993, 1996, 1997a, b; Deltchev & Curcic 1997; Deltchev & Paraschi 1990; Thaler 1996; Thaler & Knoflach 1991, 1993, 1995; Wunderlich 1980, 1985, 1994a, b, c). These contributions are a result of intensive faunistic research; and the accumulation of new data makes possible a critical taxonomic and faunistic review, together with a zoogeographical analysis.

STUDY AREA

The Balkan Peninsula is situated in the southeastern part of Europe. The northern border follows the rivers Danube (including its delta), Sava and Soca, and through Gorizia and Monfalcone reaches the line of the Gulf of Trieste. Its western border follows the line of Adriatic and Ionian coast including the islands. The eastern border passes to the east of the Aegean Islands Sirina, Astipalea, Amorgos, Miconos, Tinos, Andros, Skiros, Limnos, and Imros, continues along the Dardanelles, goes across the Marmara Sea and, through the Bosphorus, reaches the Black Sea coast. The southernmost point of the Balkan Peninsula region is Crete and the islands of Gavdos, Aiduronisi, and Kufonisi (Fig. 1).

The material treated herein can be divided into two major parts: the first comprises a critical incorporation of all available records from the literature concerning the distribution of spiders on the Balkan Peninsula; the second concerns a revision of all of the existing material from Drensky's collection.

The geographical areas and their abbreviations used in the text, are as follows: Al = Albania, BG = Bulgaria, CT = Crete, CR = Croatia, GR = Greece, BS = Bosnia, MA =

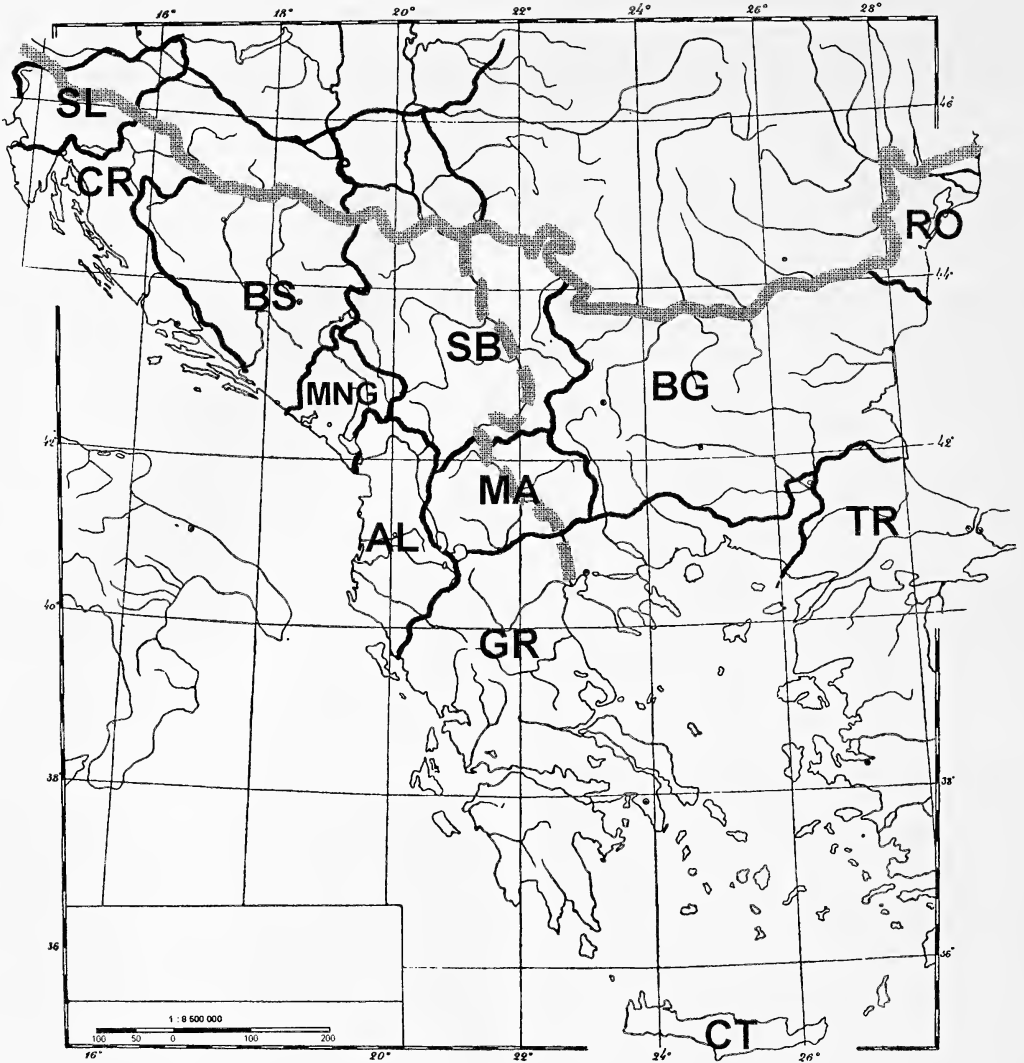


Figure 1.—Map of the Balkan Peninsula. *Abbreviations:* Al = Albania; BG = Bulgaria; CT = Crete; CR = Croatia; GR = Greece; BS = Bosnia; MA = Macedonia; MNG = Montenegro; RO = Romania; SB = Serbia; SL = Slovenia; TR = Turkey.

Macedonia, MNG = Montenegro, RO = Romania, SB = Serbia, SL = Slovenia, and TR = Turkey. The data concerning the general zoogeographical distribution are taken mainly from Platnick (1989, 1993, 1997). The zoogeographical categories used and their abbreviations are as follows: WD = widely distributed, COS = cosmopolitan, PPT = Palearctic-Paleotropic, H = Holarctic, OW = Old World, P = Palearctic, WP = west Palearctic, ECA = European-central Asian, E = European, HE = Holo-European, MEE = middle east-European, MSE = middle south European; MSEE = middle southeast European,

EE = east European; SE = south European, SEE = southeast European, PO = Pontic, BK = Balkans, M = Mediterranean, HM = Holo-Mediterranean, EM = east Mediterranean, NM = north Mediterranean, NEM = north-east Mediterranean, SEM = southeast Mediterranean, BKMA = Balkan-Asia Minor, POM = Pontic-Mediterranean.

RESULTS AND DISCUSSION

Species composition.—The spider fauna of the Balkan Peninsula is represented by 1409 species, included in 337 genera and 47 families (Table 1). This number is established after

Table 1.—The families and number of species and endemic taxa.

Family	Number of species according to Drensky (1936)	Actual number of species	Actual number of endemic species	Actual number of endemic genera
Atypidae	2	2		
Ctenizidae	5	6	5	
Nemesidae	4	7	4	
Filistatidae	4	3		
Sicaridae	1	1		
Scytodidae	1	1		
Leptonetidae		18	18	3
Pholcidae	6	16	9	
Segestridae	4	5	2	
Dysderidae	40	106	81	9
Oonopidae	1	5	2	
Palpimanidae		1		
Mimetidae	4	5		
Eresidae	2	3		
Oecobiidae	1	4		
Uloboridae	5	6		
Nesticidae	6	9	6	2
Theridiidae	80	91	9	
Theridiosomatidae	1	1		
Anapidae	1	2	1	
Mysmenidae		1		
Linyphiidae	172	330	112	3
Tetragnathidae	17	26	1	
Araneidae	60	55		
Lycosidae	80	83	1	
Pisauridae	4	3		
Oxyopidae	3	3		
Zoropsidae		1		
Agelenidae	32	64	36	1
Cybaeidae	2	4	1	
Argyronedidae	1	1		
Desidae		1		
Hahnidae	8	12	5	1
Dictynidae	15	23	1	
Amaurobiidae	24	37	19	
Titanoecidae	6	6		
Anyphoenidae	2	2		
Liocranidae	22	19	4	
Clubionidae	29	36	3	2
Corinnidae	3	3		
Zodariidae	11	23	9	
Prodidomidae		2		
Gnaphosidae	110	131	22	
Zoridae	4	10	2	
Heteropodidae	6	5	2	
Philodromidae	45	37	2	
Thomisidae	55	70	4	
Salticidae	140	130	14	

Table 2.—Distribution of species and endemic taxa in different regions of Balkan Peninsula.

Region	Number of species according to Drensky (1936)	Actual number of species	Actual number of endemic species	Actual number of endemic genera
Solvenia	108	216	26	3
Croacia	466	615	66	4
Bosnia	42	87	42	2
Serbia	453	508	10	
Montenegro	15	102	29	3
Macedonia	455	394	21	1
Albania	7	73	10	2
Bulgaria	697	775	55	2
Romainia	35	47	7	1
Turkey		83	5	
Greece	241	642	156	
Crete		59	42	4

a critical review of all available records from the literature concerning the spiders in the Balkan Peninsula and a revision of all existing materials of Drensky's collection.

The number of species is high compared with the number of spiders recorded from other parts of Europe: France -1400 (Jones et al. 1990); Russian Plain -1001 (Michailov 1997); Alps -1000 (Thaler 1980); Germany -925 (Koponen 1993); Switzerland -875 (Maurer & Hanggi 1990); England & Wales -624 (Roberts 1987). The number of families is also high compared with the data for the world - 95 (Platnick 1997); Switzerland -39 (Maurer & Hanggi 1990); Russian Plain -35 (Michailov 1997). Best represented are the families Linyphiidae (327 species or 23.4%), Salticidae (130 species or 9.3%), Gnaphosidae (129 species or 9.2%) and Dysderidae (106 species or 7.6%). The genera with the highest number of species are: *Troglohyphantes* (53), *Lepthyphantes* (49), *Dysdera* (38), *Zelotes* (38), *Xysticus* (37), *Pardosa* (35) and *Tegenaria* (31). The genus *Troglohyphantes* is a remarkable faunistic phenomenon since from all 53 species 52 are the Balkan endemics, distributed mainly in caves. Deeleman-Reinhold (1978) concluded that the present distribution and morphological diversity of *Troglohyphantes* in the Balkan Peninsula represents of a repeated processes of expansion and contraction of its range. The representation of the genera *Dysdera* (28 endemics of 38 species), *Lepthyphantes* (18 endemics of 49 species) and *Tegenaria* (17 endemics of 31 species) is also due to expansion in caves, woodlands and

highlands. Present-day examples of cave penetration are the species *Lepthyphantes centromeroides* and *L. spelaeorum*, comparatively widespread in the Balkan peninsula. They occur in caves but also in the humus and ground detritus, and active subterranean colonization is indicated (Deeleman-Reinhold 1978).

The highest number of species is recorded for the territories of Bulgaria (775), Greece (642), Croatia (614) and Serbia (508). This richness, however, depends not only on the size of the regions, but also on the degree of exploration by araneologists (Table 2). The territories of Albania, Turkey, Montenegro and Bosnia are less well-explored.

Zoogeographical analysis.—According to their current distribution, the established 1409 species can be classified into 24 zoogeographical categories, grouped into 4 complexes (Figs. 2, 3).

Best represented is the complex of widely distributed species (WD) (COS + PPT + H + OW + P + WP + ECA), represented by 533 species (38.1%). Within the WD complex, Palearctic species are dominant (75.4%), followed by Holarctic (19.9%), Cosmopolitan (3.8%) and Palearctic-Paleotropic (0.2%). The complex includes especially widespread species associated with lowlands, buildings, woodlands and high altitude zones of mountains.

The Balkan endemics complex (BK) forms the second largest group and comprises 379 species (26.9%). The established number is high and reflects the local character of the fau-

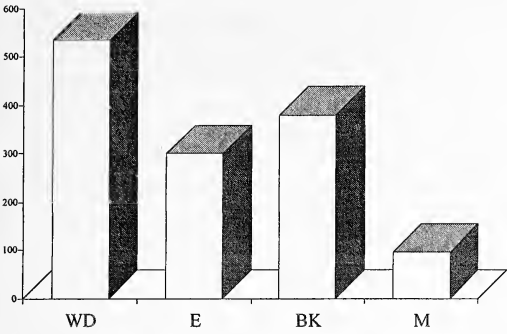


Figure 2.—The main zoogeographic complexes in the spider fauna in Balkan Peninsula, showing the number of species represented in each.

na. The endemics are best represented in Greece (156), Croatia (66), Bulgaria (55), Bosnia (42) and Crete (40). It should be emphasized that of the established 14 endemic genera (*Antrohyphantes*, *Barusia*, *Cryphoeicina*, *Fageiella*, *Folkia*, *Icariella*, *Lasconia*, *Macedoniella*, *Minotauria*, *Protoleptoneta*, *Parastalita*, *Rhodera*, *Stalagtia*, *Sulcia*) for the Balkan Peninsula, only three of them (*Antrohyphantes*, *Macedoniella*, *Protoleptoneta*) are distributed in the east of the Balkan Peninsula. Especially interesting is the distribution of the genus *Antrohyphantes*, found only at high altitude zones and caves of the eastern part of the region (Bulgaria). It is related to the genus *Fageiella*, an endemic from the

caves of the western part of the Balkan Peninsula (Bosnia, Montenegro). Their allopatric distribution indicates that they had already separated before the establishment of the Vardar tectonic zone (Deltshv 1996). This suggests that these two genera are paleoendemics.

The largest fraction of endemics was encountered mainly in caves, coastal sites, woodlands and high altitude zones. According to their ranges, the endemics belong to two principal faunistic complexes: Mediterranean and European. The Mediterranean elements are distributed in caves, forests, coastal sites and high altitudes, while the European elements are distributed mainly in high altitude sites and forests. This phenomenon can be regarded as a result of the relative isolation of the mountains compared with the lowlands, in the context of paleo-environmental changes since the Pliocene (Deltshv 1996).

The European complex (E) (HE + MEE + MSE + MSEE + EE + SEE + PO) includes 300 species (21.3%). Within it, the Holo-European species are dominant (72.7%), widespread mainly in mountains. The middle southeast European (9.0%), southeast European species (9.0%), and east European species (7.4%) are comparatively well represented. The complex comprises widespread spiders in Europe and the Balkan Peninsula which inhabit both lowlands and mountains.

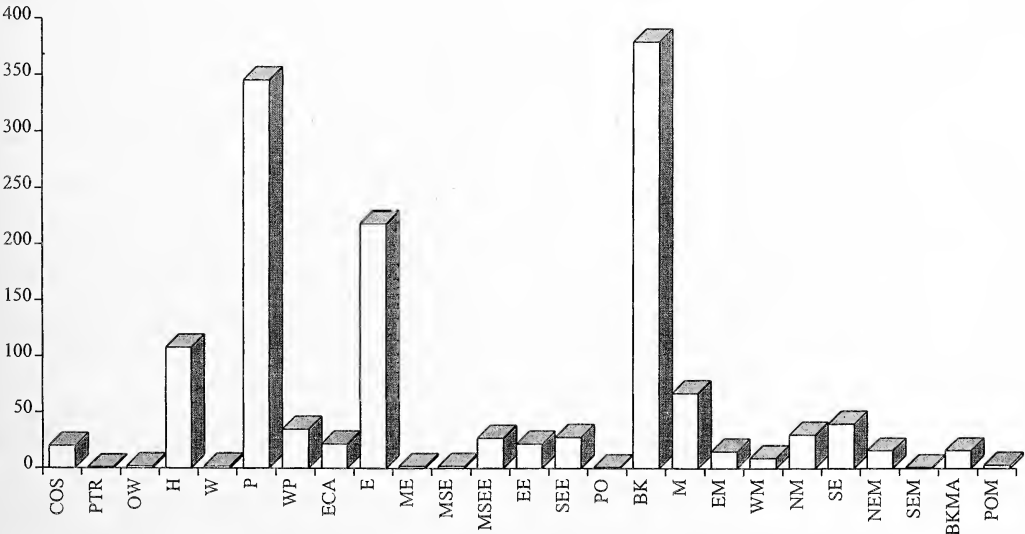


Figure 3.—Zoogeographical types in the spider fauna in Balkan Peninsula, showing the number of species represented in each.

Interesting is the group of European mountain species, best represented in the forest and sub-alpine belts.

The last complex (M) includes 195 species that occur in the Mediterranean area (HM + EM + WM + NM + SE + NEM + SEM + BKMA + POM) or a part of it. This complex forms 13.8% of the total spider fauna of the Balkan Peninsula, but the real percent is probably much higher because a large part of the Balkan endemics have a Mediterranean origin. Most of these species are widely-distributed in the Mediterranean region. Very interesting are the mountain-Mediterranean species (*Aculepeira talishia* and *Pardosa incerta*), which may be regarded as ancient elements in the high mountains.

Conclusions.—The faunistic diversity of the 1409 spider species shows that the Balkan Peninsula is a territory of considerable species richness. This conclusion is supported also by the existence of 379 endemic species. The uneven species richness in different parts of the Balkan Peninsula is due mainly to the degree of exploration by researchers. In a zoogeographical respect, the widely distributed spiders (WD) are dominant. However, the most characteristic faunal element is the Balkan endemics (BK). Their number is high, and their faunistic composition reflects the local character of the fauna. This phenomenon can be explained by the relative isolation of the mountains compared with the lowlands, in the context of paleo-environmental changes that have occurred since the Pliocene. The high percentage of the Balkan endemics (26.9%) suggests an important process of autochthonous speciation. Thus, the existing data suggest that the Balkan Peninsula represents one of the main centers of speciation in Europe.

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Spiders in Agroecosystems: Ecological Processes and Biological Control

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Frontispiece:—The spider *Tetragnatha laboriosa* Hentz (Araneae: Tetragnathidae). This long-jawed orb-weaver is ubiquitous and abundant in North American agroecosystems. The prey in the snare is a greenbug, *Schizaphis graminum* (Rodani) (Insecta: Aphididae), a cereal pest throughout Europe, Asia, Africa and the Americas. Photo by Scott Bauer, Agricultural Research Service, United States Department of Agriculture.

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WHY A SYMPOSIUM ON SPIDERS IN AGROECOSYSTEMS NOW?

Matthew H. Greenstone and Keith D. Sunderland

Our goal in organizing this international symposium was to bring together active workers to summarize what we know of the individual, population, and community ecology of spiders in agroecosystems, and to suggest how that knowledge can be used to increase the efficacy of spiders as biological control agents.

There are at least three reasons why this is an opportune time to hold the present symposium. First, there is an urgent need, and a general climate of acceptance, for the use of biological control agents in insect pest management. Second, there is ample rigorous experimental evidence that spiders *can* be effective in suppressing pest populations and improving crop health and productivity. Finally, spiders *have been* effectively incorporated into one of our important pest management systems.

Need: Despite some narrowing in the disparity between birth and death rates (Bongaarts 1998), the human population continues to grow beyond its present six billion, which already strains the ability of agriculture to provide for its food and fiber needs. The food necessary to support our growing population will have to come from increased yields on land already under cultivation (Brown 1995; Daily et al. 1998). Leveling off of crop yield increases worldwide suggests that physiological limits to photosynthesis, and to photosynthate allocation to edible plant parts, are being approached (Brown 1998; Calderini & Slafer 1998). It will take great ingenuity to increase the efficiency of use of inputs (mechanical energy, fertilizer, water, pesticides and other pest management tools, crop and livestock genetic diversity) while reducing environmental and social costs (soil erosion and salinization, lowering of water tables, soil and water pollution, loss of biodiversity, development of pesticide and antibiotic resistance) (Daily et al. 1998).

Each agricultural discipline has a role to

play in the optimization of variables affecting food availability. As ecologists who study a group of obligate insectivores, arachnologists' obvious arena is pest management. More than 600 arthropod pest species regularly take more than 10% of our agricultural production (Samways 1997). Total reliance on synthetic chemical pesticides for pest suppression entails many severe and costly health, environmental, and even pest management side effects (Newsome 1970; Kaaya 1994; Pimentel et al. 1992). Genetic engineering of crops is not a magic bullet to solve this problem. The most widely touted approach, insertion of microbial insecticidal genes into crop plants, requires complex region-wide management schemes to ensure its sustainability (Gould 1998), and it is being broadly resisted by environmentalists.

The insecticide crisis has led to a broader acceptance of Integrated Pest Management (IPM), including the addition or enhancement of natural enemy populations (Andow & Rosset 1990). Insect natural enemies, particularly parasitoids and pathogens, are well-recognized components of IPM programs. Spiders, despite their ubiquity and high densities (Dondale 1970; Turnbull 1973; Nyffeler & Benz 1987), have not received the recognition they need in order to be fully utilized in this enterprise, although their treatment in several recent compendia is encouraging (Toft & Riedel 1995; Booij & den Nijs 1996; Powell 1997; Barbosa 1998).

Evidence for potential effectiveness of spiders as biological control agents: Many field experiments, performed over the last 35 years, have demonstrated that spiders can reduce insect populations and the crop damage they cause (Itô et al. 1962; Mansour et al. 1980; Mansour & Whitcomb 1986; Mansour 1987; Orazé & Grigarick 1989; Riechert & Bishop 1990; Carter & Rypstra 1995; Riechert & Lawrence 1997). At least one of these exper-

iments contains implicit, applicable protocols for increasing vegetable productivity by altering the microhabitat at the soil surface to make it more attractive to spiders (Riechert & Bishop 1990).

Spiders have been incorporated into one important pest management system: An abundant wolf spider, *Lycosa (Pardosa) pseudoannulata*, is among the arthropods counted by rice farmers in the FAO Intercountry Programme for Integrated Pest Control in south and southeast Asia when they make management decisions for brown planthopper and other insect pests (Stone 1992). One reason this program has been so successful is that farmers learn its worth by performing field experiments (Ooi 1996).

Organization of the symposium.—We devised a framework to enable us to get from basic ecological principles to the enhancement of the role of spiders as biological control agents. A few subject areas had to be omitted due to other commitments of potential contributors. With these few exceptions, we believe we were able to touch on most of the important principles and applications. Surprisingly, some of the most important questions either had not been examined or had only been cursorily examined before. We therefore had to challenge some of our colleagues to take on topics for which the conclusions were not obvious in advance. That these efforts produced a number of startling and provocative insights is a source of great satisfaction to us.

To ensure rigor and completeness, all papers were subjected to external peer review by leaders in their fields.

Coda.—Agroecosystems, though mind-numbingly complex, are simpler than most natural ecosystems and more amenable to experimental manipulation. Therefore they are convenient and tractable outdoor laboratories for invertebrate ecologists. Furthermore the existence of data, methodologies and models concerning pests and natural enemies obviates the need for much initial groundwork. We encourage more ecologists to work in these important systems.

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GUILD STRUCTURE OF SPIDERS IN MAJOR CROPS

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ABSTRACT. The ecological guild concept has been of great interest to arachnologists, and the different manner in which spiders forage for a common resource—prey arthropods—has led to numerous attempts to classify them into guilds. However, questions have been raised about the validity of guilds and the taxon-centered basis of their definition. Here, we propose an alternative approach to guild classification, using quantitative analysis of ecological characteristics of spider families. While generalizations may not apply to all species within a taxon, results from this approach suggest eight major spider guilds similar to earlier guild assignments by some authors and provide a reasonable framework for future studies. We used this classification in a comparison of spider guild composition across several major crops (from published studies). While total species richness varied widely among crops, the proportion of the total species within each guild was remarkably even across crops. The relative abundance of guilds (based on numbers of individuals) varied greatly, which may reflect availability of resources within a crop type. Patterns of similarity in guild composition suggest the possibility of plant habitat structure as an influence on the spider community. Further detailed analyses of spider guilds in various crops have been constrained by both a lack of comparable quantitative data and the paucity of behavioral and natural history information available for many taxa. As recent studies have shown that assemblages of spiders can impact pest populations and reduce crop damage, a better understanding of spider guild composition and variation in spider community structure among crops is essential in future studies of the arthropod fauna in agroecosystems.

The guild concept.—The concept of the ecological guild—a group of species utilizing the same resource in similar ways—has its origins in early plant and animal ecology, when ecologists recognized the organization of trophic groups called “Genossenschaften” (Schimper 1903) and “Syntrophia” (Balogh & Loksa 1956). Modern usage of the term “guild” was formalized in a study of avian niche exploitation patterns as “a group of species that exploit the same class of environmental resources in a similar way” (Root 1967) and this concept was later extended to the arthropod fauna of collards (Root 1973). An assumption derived from competition theory is that species within guilds are most likely competitors, therefore guilds are suggested to form the basis of community organization. Since its inception, the guild concept has been applied to numerous animal and plant com-

munities (e.g., see reviews in Hawkins & MacMahon 1989; Simberloff & Dayan 1991).

While many studies concerning guild structure of communities exist, there has been much debate over guild definitions and the circumstances under which the concept should be used. Criticisms include the lack of formal or testable definitions (Adams 1985) and misuse by investigators using taxon-centered *a priori* guild assignments (Jaksić 1981; Hawkins & MacMahon 1989; Jaksić & Medel 1990). Hawkins & MacMahon (1989) argue that while guilds constitute an ecologically appropriate context in which to study interspecific competition and complex interactions among species, most guild-centered approaches misdefine guilds, as the key element is the *resource* (e.g., “does it matter that a particular insect species is captured by a silken spider web or a bird’s beak”?) and *not* the similar manner of utilization (behavior). Simberloff & Dayan (1991) agree that taxocenes do not necessarily equal guilds, but to be properly defined, a guild must meet *both* criteria: species

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using the “same class” of resources in a behaviorally “similar way.”

Since related species often use resources in a similar manner, guilds will reflect taxonomic relationships; distantly related taxa may not necessarily belong to the same guild, even if they use similar resources (but see Jaksic (1981)). Jaksic (1981) and Jaksic & Medel (1990) suggest there may be two types of guilds: (A) Community guilds (“true” guilds that are syntopic, resource-based and independent of taxon or trophic level *sensu* Root (1967)); and (B) Assemblage guilds (taxon-based guilds comprising related species). These authors admonish researchers to identify the resource in question first, then construct guilds by quantitative analysis of resource acquisition.

Spider guilds.—Arachnologists have widely embraced the guild concept, as the different manners in which spiders forage for a common resource—prey arthropods—is obvious. Not surprisingly, there have been numerous attempts to classify spiders into as few as two and as many as 11 guilds, with varying degrees of specificity (Table 1). As with other taxa, problems arise assigning species to particular guilds, for generalizations based on higher taxa may not apply to all species. For example, *Castianeira* (Clubionidae) and *Sergiolus* (Gnaphosidae) are similar—diurnal, ant-mimicking species—but their families are often placed in a “nocturnal” guild (e.g., Post & Riechert (1977) designate these as “nocturnal running spiders”). In addition, some taxa within a particular family (e.g., Clubionidae) may forage primarily on vegetation (e.g., *Cheiracanthium*, *Clubiona*) whereas others may be ground-dwellers (e.g., *Castianeira*, *Phrurotimpus*) (Whitcomb et al. 1963). Some members of web-building spider families such as Linyphiidae, Agelenidae and Hahniidae may move frequently and often forage off of the web, while others are sedentary. The family Lycosidae poses particular problems. For example, some lycosids are diurnal (e.g., *Schizocosa*, *Pardosa*) while others are nocturnal (e.g., *Rabidosia*). Others forage as sit-and-wait ambush predators at a burrow entrance (e.g., *Geolycosa*) while others actively move about in search of prey (e.g., *Schizocosa*, *Pardosa*). Some species, like *Hogna helluo*, actively disperse and change sites at night, but forage in a sit-and-wait manner during the day (Mar-

shall pers. comm.). Ideally then, guild membership should reflect the natural history and behavior of single species; but such precision is not realistic as such data are presently not available for most families.

Determination of spider guilds.—Before we can attempt to define spider guilds in major agricultural crops, several key questions must be addressed: (A) Do all spiders in an agricultural field exploit the “same class” of resources? As spiders are generalist predators of arthropods, the argument can be made that this is true despite the diversity of trophic levels (e.g., herbivores, detritivores, parasitoids, predators) the prey represent. (B) At what level do different foraging strategies affect resource utilization and thereby constrain or subdivide the “same class” of resources? While at some level, nocturnal vs. diurnal or web-building vs. hunting species surely exploit different prey resources, degrees of prey specialization appear to vary widely at the species level; and data are lacking entirely for many higher taxa. Syntopic species representing different foraging strategies or distinct web structures may show great prey variability and could be considered to exploit different resource classes (Nyfeller et al. 1989). Other studies show considerable overlap in spider diets despite major differences in web structure and microhabitat use (Wise & Barata 1983; Riechert & Cady 1983). At the same time, even syntopic species exhibiting very similar foraging strategies may consume different types of prey and significantly vary in their level of polyphagy (e.g., *Oxyopes salticus* and *Peucetia viridans* lynx spiders in cotton (Nyfeller et al. 1992)). (C) Since there are numerous other taxa of generalist predatory arthropods in a crop field, are spiders part of a larger guild set? This would depend on whether the focus is on “community” or “assemblage” guilds, *sensu* Jaksic (1981). Spiders as a group clearly represent the latter case, and given our arachnocentric focus and the potential importance of spiders in pest management, use of this term may be well-justified.

These questions are the essence of the guild conundrum for arachnologists, and the potential for circular reasoning is high. We justify our approach as follows. First, the primary focus of research on arthropods in agriculture is pest management. Since agroecosystems are

Table 1.—Existing spider guild classifications.

Spider family	Guild classification of spider taxa and the number of recognized guilds	
	Uetz 1977 (2 guilds)	Post & Riechert 1977 (11 guilds)
Pholcidae	Web-builders	—
Theridiidae	Web-builders	Scattered-line weavers
Dictynidae	Web-builders	Hackled band weavers
Linyphiidae	Web-builders/Wandering	Sheet line weavers
Micryphantidae	Web-builders/Wandering	Sheet line weavers
Hahniidae	Web-builders/Wandering	Hahniid spiders
Amaurobiidae	Web-builders	—
Filistatididae	Web-builders	—
Agelenidae	Web-builders	Funnel web spiders
Araneidae	Web-builders	Orb weavers
Tetragnathidae	Web-builders	Orb weavers
Uloboridae	Web-builders	—
Anyphaenidae	Wandering spiders	Nocturnal running spiders
Clubionidae	Wandering spiders	Nocturnal running spiders
Gnaphosidae	Wandering spiders	Nocturnal running spiders
Lycosidae	Wandering spiders	Diurnal running spiders
Dysderidae	Wandering spiders	—
Pisauridae	Wandering spiders	—
Oxyopidae	Wandering spiders	Diurnal running spiders
Salticidae	Wandering spiders	Jumping spiders
Philodromidae	Wandering spiders	—
Thomisidae	Wandering spiders	Crab spiders
Heteropodidae (Sparassidae)	Wandering spiders	—
Sparassidae	Wandering spiders	—

human-managed monocultures, the arthropod “communities” they support are somewhat artificial, i.e., they represent temporary assemblages of taxa drawn together as a consequence of a variety of factors without a long history of evolutionary interactions.

Second, spiders colonizing agricultural fields are mostly generalist predators of arthropods (including other spiders); and while they may have evolved their particular niche exploitation patterns under different ecological circumstances, they exploit the same class of resources. Since the potential prey of spiders in agroecosystems may vary with microhabitat, season, time of day, and foraging strategy, spiders may constitute more than one “assemblage guild.” Under this set of circumstances, guilds will strongly mirror taxonomic relationships.

Finally, several recent studies have shown that assemblages of generalist predators (especially spiders and carabid beetles) can impact pest populations and reduce crop damage

(Riechert & Bishop 1990; Snyder & Wise pers. comm.). Thus, an understanding of how spider assemblages in agroecosystems are organized is essential to study and employ these predators as pest control agents.

We will attempt here to construct spider guilds that may be found in agricultural fields. It should be made clear that these are preliminary designations, as data are often anecdotal and limited to a few representative species in any given family. New information on foraging behavior and microhabitat utilization patterns may change the basic assumptions. We will base our analysis on spider families, despite our own concerns about generalizations, because at least some information is available for each of the families commonly found in agroecosystems.

METHODS

Guild classification.—Spider families used in the determination of guilds were those listed as occurring in U.S. field crops cited in the

Table 1.—Extended.

Guild classification of spider taxa and the number of recognized guilds		
Nyffeler 1982 (3 guilds)	Riechert & Lockley 1984 (8 guilds)	Young & Edwards 1990 (5 guilds)
—	Scattered Line Weavers	Web-Matrix
Space-web spiders	Scattered Line Weavers	Web-Matrix
Space-web spiders	Hackled-Band Weavers	Web-Sheet
Space-web spiders	Sheet Web Builders	Web-Sheet
Space-web spiders	—	—
—	—	Web-Sheet
—	Sheet Web Builders	Web-Sheet
—	—	Web-Sheet
Space-web spiders	—	Web-Sheet
Orb Weavers	Orb Weavers	Web-Orb
Orb Weavers	Orb Weavers	Web-Orb
—	Orb Weavers	Web-Orb
—	Nocturnal Running	Wandering-Active
Hunting spiders	Nocturnal Running	Wandering-Active
—	Nocturnal Running	Wandering-Active
Hunting spiders	Diurnal Running	Wandering-Active
—	—	Wandering-Active
Hunting spiders	Diurnal Running	Wandering-Active
—	Diurnal Running	Wandering-Active
Hunting spiders	Jumping	Wandering-Active
—	Crab	Wandering-Active
Hunting spiders	Crab	Wandering-Ambush
—	Crab	Wandering-Ambush
—	Crab	Wandering-Ambush

review of Young & Edwards (1990). To our knowledge, their study constitutes the most comprehensive treatment of spider species composition in agroecosystems available. Designation of spider guilds was based on ecological characteristics known for the family, or for a key species representing each family (Gertsch & Riechert 1976; Post & Riechert 1977; Gertsch 1979; Young & Edwards 1990; Nyffeler & Benz 1987; Nyffeler et al. 1992; Uetz, Halaj & Cady pers. obs.). Ecological characteristics relating to foraging manner, web type, microhabitat use, site tenacity and diel activity (Table 2) were subjected to a hierarchical cluster analysis using the unweighted pair group method with arithmetic averages using the MEGA software package (Kumar et al. 1993). Output of the analysis was organized into a dendrogram, and subsequent guild designations were based on the relative similarity of spider family clusters.

Spider guilds in agroecosystems.—We analyzed the dataset compiled by Young & Ed-

wards (1990) to compare species richness of spider guilds among major U.S. crops. We also gathered additional information from literature cited within and from other sources to obtain quantitative data on spider guild structure of major crops. Here, relative abundances of spider guilds were averaged across: (1) same-crop references, and (2) datasets derived from several sampling techniques employed in the same study (e.g., sweeping vs. pitfall trapping), respectively, to obtain a more meaningful estimate of spider assemblage structure for a particular crop.

Analyses.—The similarity in spider species richness among crops was evaluated with the Sørensen qualitative coefficient C_s (Southwood 1992). We used our proposed guild classification to compare spider assemblage structure among individual crops using the species richness and spider abundance data. Similarity in spider guild composition was calculated with the proportional similarity index PS (Price 1984; Smith 1996). The similarity

Table 2.—Criteria used to construct new spider guild classification. 0 and 1 designate the absence of presence of the ecological characteristic, respectively, unless stated otherwise. Web use: 0—none; 1—sit on web; 2—hunt off web. Plant use: 0—none; 1—on foliage; 2—between plants. Site tenacity: 0—sedentary; 1—frequent site change; 2—mobile.

Family	Web	Web use	Tube web	Sheet web	Sheet/ space web
Agelenidae	1	1	0	1	0
Amaurobiidae	1	1	0	1	0
Anyphaenidae	0	0	0	0	0
Araneidae	1	1	0	0	0
Clubionidae	0	0	0	0	0
Dictynidae	1	1	0	0	0
Dysderidae	0	0	0	0	0
Filistatidae	1	2	1	0	0
Gnaphosidae	0	0	0	0	0
Hahniidae	1	2	0	1	0
Linyphiidae	1	2	0	0	4
Lycosidae	0	0	0	0	0
Micryphantidae	1	2	0	0	0
Mimetidae	0	0	0	0	0
Oxyopidae	0	0	0	0	0
Philodromidae	0	0	0	0	0
Pholcidae	1	1	0	0	0
Pisauridae	0	0	0	0	0
Salticidae	0	0	0	0	0
Sparassidae	0	0	0	0	0
Tetragnathidae	1	1	0	0	0
Theridiidae	1	1	0	0	0
Thomisidae	0	0	0	0	0
Uloboridae	1	1	0	0	0

among crops was then expressed in a form of dendrogram, with clusters constructed using the unweighted average linkage method (Pielou 1984). Cluster analyses were performed with STATISTICA (StatSoft 1997).

RESULTS AND DISCUSSION

Proposed guild classification.—The hierarchical cluster analysis produced a dendrogram which we used to construct spider guilds (Fig. 1). The breakdown of successive clusters appears to be based primarily on web use, web type, and microhabitat (but not diel activity), resulting in 6–8 clusters of spider families that can be considered guilds. The families of spiders separate first into web-building and hunting groups, and are further subdivided into clusters with obvious foraging similarities. Within the hunting spiders, two or four guild designations are possible, as a running spider cluster is distinct from a stalking/ambushing cluster; but separate guilds for foliage runners, ground runners, stalkers and ambushers can be

designated within each of these clusters respectively. Within the web-building spiders, four distinct clusters correspond to previously-designated guilds (Riechert & Lockley 1984; Young & Edwards 1990): sheet web builders, wandering sheet/tangle weavers, orb weavers and 3-D space web builders.

Patterns of spider species richness in major crops.—The surveyed crops fall into three basic categories in terms of their spider fauna richness as suggested by Young & Edwards (1990). Cotton, soybean, and alfalfa support the highest number of spider species, followed by sugarcane, corn and peanut. Sorghum, rice and guar are the most species-poor crops (Fig. 2A). Besides vast differences in species richness, spider faunas of individual crops were also distinctly dissimilar (Fig. 2A). With the exception of alfalfa and soybeans (59.4% of species in common), values of species similarity were less than 45.0% for most crops. Since the vast majority of spider fauna in agricultural systems originates in natural habi-

Table 2.—Extended.

Space web	Orb web	Ambush	Stalk	Pursue	Ground	Vegetation	Plant use	Site tenacity	Diurnal	Nocturnal
0	0	0	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	0	0	1
0	0	0	0	1	0	1	1	2	0	1
0	1	0	0	0	0	1	2	1	1	0
0	0	0	0	1	0	1	1	2	0	1
1	0	0	0	0	0	1	1	0	1	0
0	0	0	0	1	1	0	0	2	0	1
0	0	0	0	0	1	0	0	0	0	1
0	0	0	0	1	1	0	0	2	0	1
0	0	0	0	0	1	0	0	1	1	0
0	0	0	0	0	1	1	1	1	1	0
0	0	0	0	1	1	0	0	2	1	0
1	0	0	0	0	1	1	1	1	1	0
0	0	0	1	0	0	1	1	2	1	0
0	0	0	0	1	0	1	1	2	1	0
0	0	1	0	0	0	1	1	2	1	0
1	0	0	0	0	0	1	1	0	1	0
0	0	1	0	0	0	1	1	2	1	0
0	0	0	1	0	0	1	1	2	1	0
0	0	1	0	0	0	1	1	2	0	1
0	1	0	0	0	0	1	2	1	1	0
1	0	0	0	0	0	1	1	0	1	0
0	0	1	0	0	1	1	1	2	1	0
0	1	0	0	0	0	1	2	1	1	0

tats, this pattern may likely reflect regional differences in the composition of spider fauna of adjacent habitats (Yeargan & Dondale 1974; Luczak 1979).

Despite notable differences in the number of spider species found in different crops and pronounced dissimilarities in their spider faunas (Fig. 2A), a remarkable constancy in the proportion of spider species within individual guilds was uncovered across all crops (Fig. 2B). For example, on average 16.9% of all spider species across the surveyed agricultural communities were stalkers. This pattern was consistent among all crops as suggested by the relatively low value of the coefficient of variation (CV) of 18.6%. Similarly, species of ambushers, foliage runners, ground runners, and sheet-web wanderers constituted a “fixed” percentage of the crop spider fauna (Fig. 2B). To our knowledge, this is the first report of species richness constancy reported for spider guilds and suggests the classification scheme outlined here may provide a good working ba-

sis for testing the significance of this pattern across a wider range of crop communities. Despite documented cases of similar proportional constancy of species numbers in arthropod guilds in several communities, a clear explanation for this natural pattern is lacking (Heatwole & Levins 1972; Moran & Southwood 1982). Heatwole & Levins (1972) suggest that the uniformity of trophic structure may mirror the spectrum of available species colonizing the habitat. In the case of agricultural systems, this explanation would imply the presence of a proportional constancy of spider species in adjacent natural habitats, a phenomenon awaiting an explanation of its own. Species responses to particular features of the habitat, or complex community interactions, may also dictate the resulting assortment of species (Heatwole & Levins 1972; Moran & Southwood 1982).

Spider guild structure of major crops.—Spider guild structure (proportional abundance) varied among individual crops (Fig. 3).

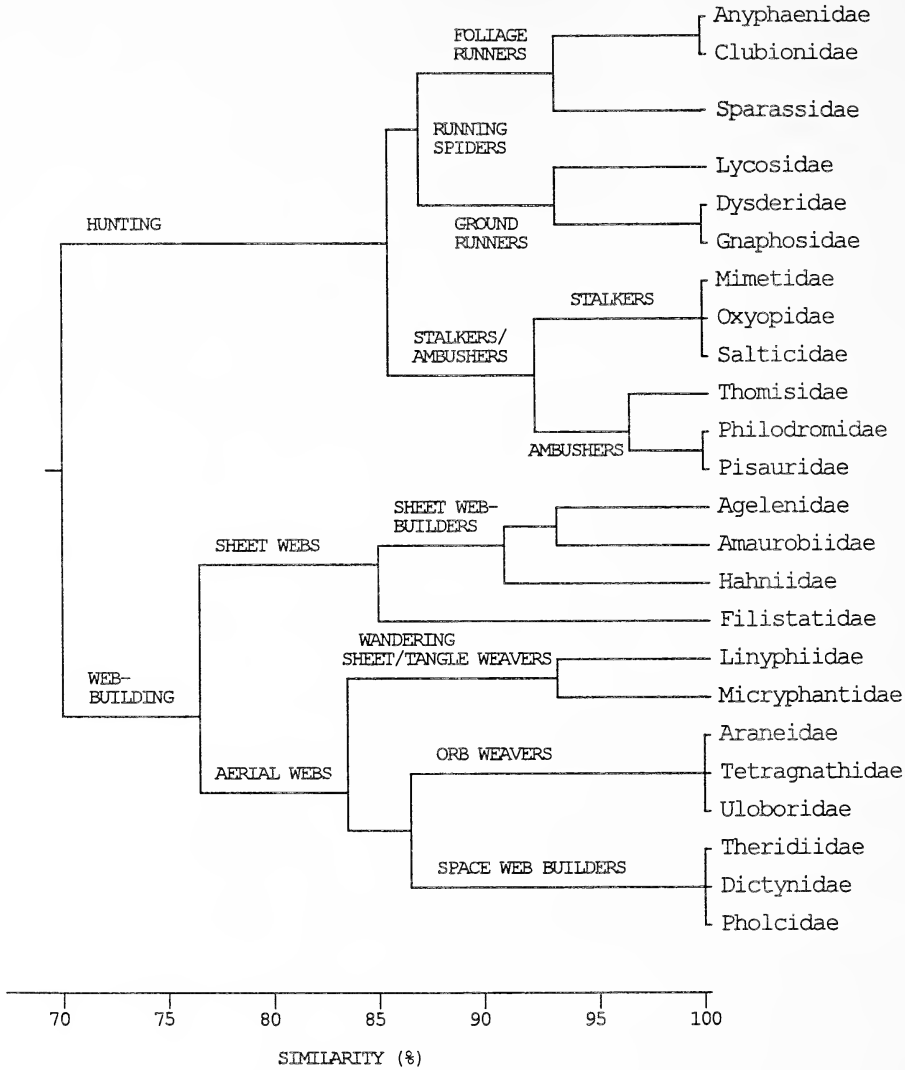


Figure 1.—Proposed spider guild classification dendrogram.

Based on structural similarity of spider guilds, two distinct groups of crops were separated: crops with spider fauna dominated by ground runners and web-wanderers (peanut, alfalfa, soybean, rice) and crops with a greater representation of orb weavers and stalkers (corn, cotton, sugar, sorghum). Similarly distinct assortments of spider guilds have been reported from a variety of crops (see reviews in Luczak 1979; Nyffeler 1982).

The most common explanation for observed patterns of spider guild structure are effects of the host-crop, including its structural diversity, microenvironment, or the level of disturbance (Luczak 1979; Young & Edwards

1990). Ample observations and more recent experimental evidence suggest that habitat structure maintains diverse spider assemblages (Uetz 1991; Wise 1993) and may be critical to successful insect suppression (Riechert & Lockley 1984; Riechert & Bishop 1990; Carter & Rypstra 1995; Marc & Canard 1997; and reviews in Wise 1993). Structural complexity may determine the guild composition of a crop's spider fauna and indirectly influence the level of herbivore damage (Young & Edwards 1990). Structurally complex crops providing a wider assortment of resources would be predicted to support a more diverse spider assemblage, thus increasing the chances of the

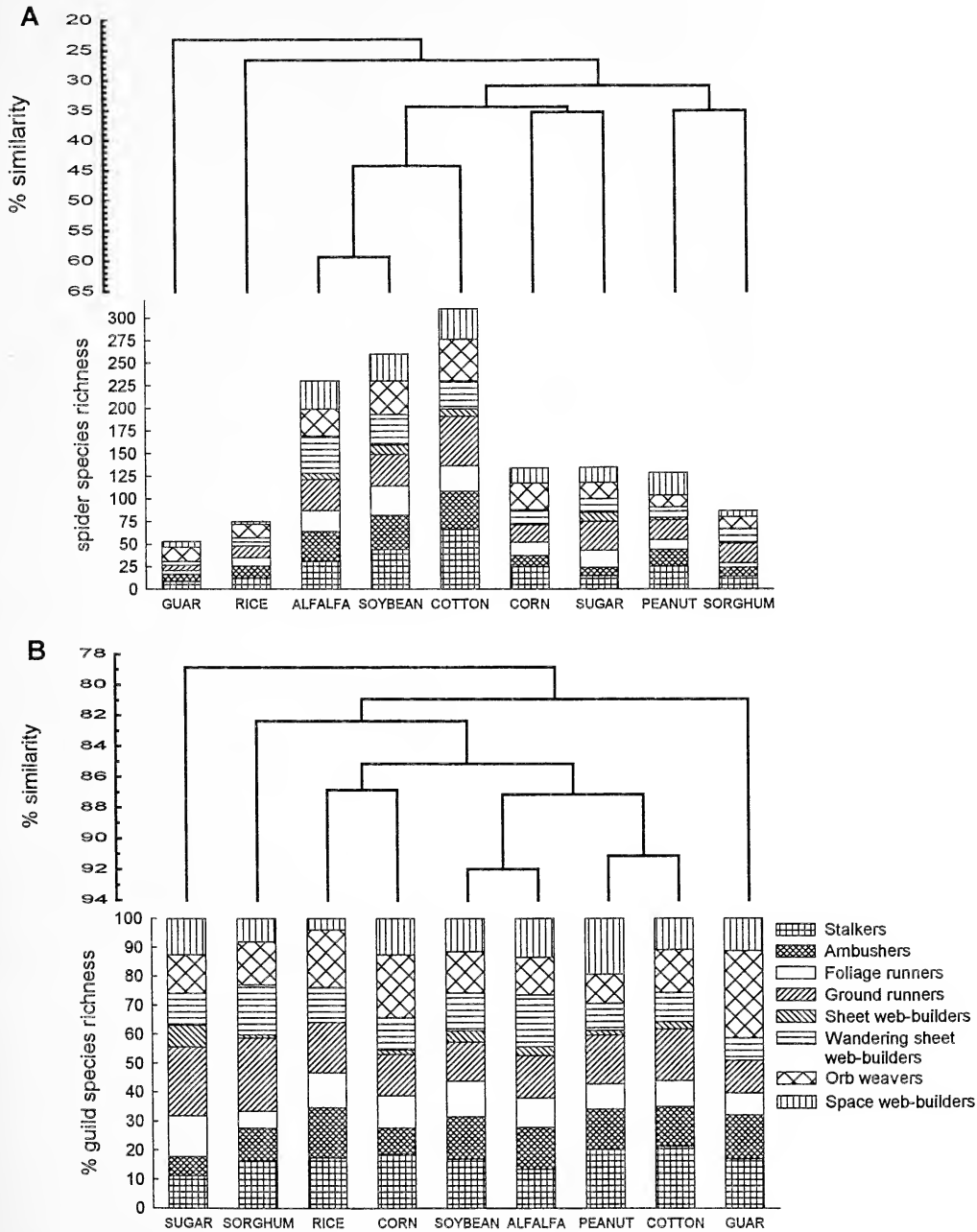


Figure 2.—A. Similarity in spider species composition among major crops. The dendrogram depicts clusters of the Sørensen qualitative coefficients. The bar graph represents the total number of spider species per guild. B. Proportional similarity (qualitative) in the relative species richness of spider guilds of major crops. The dendrogram represents clustering of values of the proportional similarity index. The bar graph shows the relative species richness of individual spider guilds. The figure is based on data in Young & Edwards (1990).

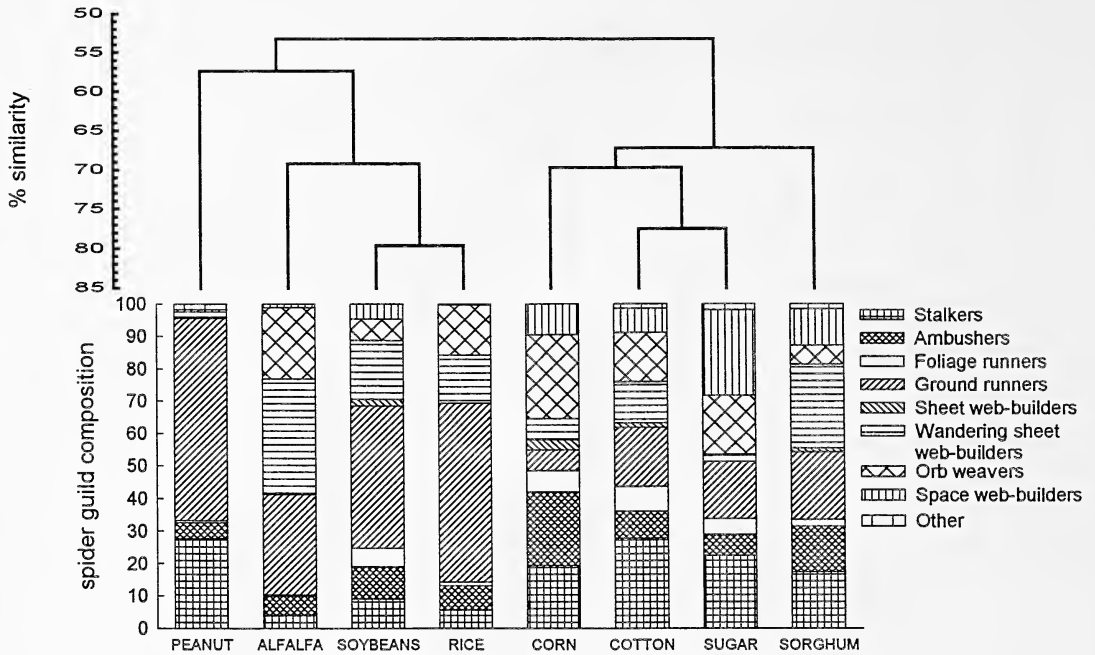


Figure 3.—Proportional similarity (quantitative) in the spider guild composition of selected crops. The dendrogram depicts clustering of values of the proportional similarity index. The bar graph represents the relative abundance of individuals spider guilds. The figure is based on data in Everly (1938); Whitcomb et al. (1963); Bailey & Chada (1968); Howel & Pienkowski (1971); Yeargan & Dondale (1974); Woods & Harrel (1976); LeSar & Unzicker (1978); Dean et al. (1982); Ferguson et al. (1984); Heiss & Meisch (1985); Agnew & Smith (1989); and Breene et al. (1993).

“best” match between spiders and insect pests. On the other hand, structurally-simple crops may not develop an abundant and species-rich spider fauna, perhaps, lowering the importance of spider predation under these conditions.

Although it is reasonable to expect a significant influence of crop characteristics on structuring the resident spider community, the importance of adjacent habitats must also be considered (e.g., Webb et al. 1984; Duelli et al. 1990). Selective forces of the crop environment can act only on “what is available,” i.e., sets of species colonizing fields from neighboring habitats. For example, spider assemblages of alfalfa fields in Virginia are dominated by orb-weaving (42.7% of total spiders) and web-wandering guilds (37.6%) (Howell & Pienkowski 1971), while the same crop grown in California, and sampled with identical techniques (sweeping and D-vac sampling), is inhabited primarily by ground-running spiders (60%) and web-wanderers (33.6%), with orb-weavers constituting less than 2.0% of all individuals (Yeargan & Don-

dale 1974). Neighboring habitats may also influence the composition of crop spider fauna indirectly by modifying the dispersal of potential spider prey and predators in the patchy agricultural landscape (Alvarez et al. 1997; Polis et al. 1997).

Future directions.—Can the spider guild structure be predicted for a particular crop system? Although some patterns emerge from available studies, reliable predictions based on the current state of knowledge are not realistic. More data based on sound experimental design, studies combining several sampling techniques and detailed observations of spider habitat selection and diets, are critically needed to address this question. This forum provides a unique opportunity to address this critical issue and encourages more extensive work on spider guilds of major crops, similar to efforts of Luczak (1979), Nyffeler & Benz (1987), or Young & Edwards (1990). The following are our pleas to the arachnological and entomological audience: (A) Quantitative estimates of spider abundance. More attention should be given to recording and publishing

quantitative information on spider guilds, as sole species composition data provide only partial answers to a multitude of questions regarding the structuring of spider guilds. (B) Observations of spider foraging and diet. Detailed observations of spider foraging and gathering of additional dietary data should be a critical component of a well-designed study. This information would help to confirm or reassess the validity of guild membership for individual spider species and further our limited knowledge of the significance of spiders as biocontrols. (C) The quality of adjacent habitats. Spider composition of the focal habitat is undoubtedly influenced by the quality of adjacent habitats via a multitude of direct or indirect channels. In order to understand the process of spider guild formation in the mosaic agricultural landscape, it is vital to record the context of crop fields as part of the sampling protocol, and if possible, to sample surrounding vegetation.

While arachnologists and others working in agroecosystems have been encouraged by results of recent studies suggesting that spiders can impact pest populations and reduce crop damage, most would agree that agricultural arachnology is still in its infancy compared with the breadth and depth of entomological research on integrated pest management and biological control. Baseline data on natural history and foraging behavior, necessary for any quantitative analyses of spider guilds within crop types, exist only for a limited number of species and are completely lacking for many spider taxa, including entire families. A better understanding of spider guilds, their composition and factors influencing spider community structure is therefore essential in future studies of the arthropod fauna of agroecosystems.

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AN AERIAL LOTTERY: THE PHYSICS OF BALLOONING IN A CHAOTIC ATMOSPHERE

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ABSTRACT. The annual recolonization of many agroecosystems by spiders is accomplished more by aerial deposition of ballooning spiders than by cursorial invasion from refugia such as forests and fence lines. The resulting spider communities can have major direct impacts on prey populations and can therefore strongly influence crop productivity. In this paper I first review what we know about ballooning in the broad sense, and then explore the influence of localized atmospheric structure on the physics and dynamics of ballooning. I used relatively high frequency measurements of air movement (speed and inclination) to develop a statistical characterization of the aerial microclimate at the top of the canopy in a field dominated by goldenrod (*Solidago* sp.), and analyzed the known physics of ballooning in the context of that statistical characterization. The major findings are (1) that the spider's perception of the current state of its microclimate, at least with respect to air direction and speed, has almost no predictive value and can only contribute to the spider's decision-making in a statistical sense, and (2) that the size distribution of the population of aeronauts is well explained by constraints imposed by aerodynamics and the probabilistic structure of the turbulent atmosphere.

The colonization of agricultural ecosystems by arthropod herbivores and their predators has attracted the attention of researchers (Southwood 1962; Bunce & Howard 1990; Wissinger 1997) in part because of the impressive economic impact that uncontrolled outbreaks of pests can cause (e.g., Andow 1991). A growing proportion of the colonization literature now concerns the sources of immigrants and the utility of manipulating the vegetational structure of agroecosystems to foster immigration of the natural enemies of herbivores (Mansour et al. 1983; Kemp & Barrett 1989; Duelli et al. 1990; Rodenhous et al. 1992; Rypstra et al. 1999, this volume).

In this context, the annual recolonization of tilled agroecosystems by spiders, which are generalized predators on arthropod herbivores, is particularly interesting. This recolonization occurs both by terrestrial locomotion, which may be diffusion-like in its dynamics (Stamps et al. 1987; Mauremooto et al. 1995), and by aerial deposition following ballooning. The importance of ballooning in influencing the population size and species composition of the arachnid fauna in these agricultural systems has only recently been recognized: Bishop & Riechert (1990) used sticky traps, pitfall traps, and exclosures to demonstrate that 41–50% of the spider species found in their plots had ar-

rived by aerial deposition, and that, in the course of the four-month growing season, the aerial deposition was occurring at a rate of at least 0.18 spider/day/m². Although that estimate seems modest, it translates into an influx of 1800 spiders into a 1-ha field during each day of the growing season, and a total influx of about 2.16×10^5 spiders over the growing season. The impact of the spider population, whatever its route of arrival, on crop productivity can be impressive (Riechert & Lockley 1984; Riechert & Bishop 1990; Carter & Rypstra 1995).

Our understanding of ballooning, the process responsible for aerial deposition, is still incomplete but is guided by a growing literature (Weyman 1993) addressing the following questions: Who are the aeronauts and why are they, and not others, airborne? Under what meteorological conditions does ballooning occur? What are the population and distribution effects of spider ballooning? How do physics and behavior interact during ballooning?

The aeronaut fauna.—Although many arthropod species are captured in aerial surveys (Greenstone et al. 1991), relatively few are both wingless and exhibit behavioral adaptations that foster aerial dispersal. Among the quasi-passive aeronauts are some that travel unaided by silk (e.g., wingless homopteran in-

Table 1.—Family-richness and dominant families in studies of airborne spiders.

Study location	Timing	Number of families	Numerically dominant taxa	Reference
Wichita Falls, Texas	year; peaks in May, September	13	Linyphiidae	Salmon & Horner 1977
College Station, Texas	year; peaks in June, September	18	Linyphiidae, Arancidae	Dean & Sterling 1985
Huntsville, Texas	April–August; peak in May	18	Linyphiidae, Araneidae	Dean & Sterling 1985
Trangie, New South Wales, Australia	November	10	Linyphiidae	Greenstone et al. 1987
Columbia, Missouri	June–October	12	Linyphiidae	Greenstone et al. 1987
Oak Ridge, Tennessee	May, June	12	Linyphiidae, Thomisidae	Bishop 1990
Oak Ridge, Tennessee	September, October	12	Thomisidae	Bishop 1990
Bellflower, Missouri	July	8	Linyphiidae	Greenstone et al. 1991

sects: Hoelscher 1967; Washburn & Washburn 1984; tetranychid and phytoseiid mites: Johnson & Croft 1976; Smitley & Kennedy 1985) and a large number for whom silk facilitates transport (lepidopteran larvae: Cox & Potter 1986; McManus & Mason 1983; spiders, below).

Quantitative aerial surveys of ballooning spiders (Table 1) have revealed a degree of family- and species-richness that was not implied by early observations of conspicuous mass-migrations (Darwin 1839; McCook 1877; Emerton 1908; Bristowe 1939; Duffey 1956). The most numerous family of aeronauts is the Linyphiidae, a family of characteristically very small spiders. The physics of ballooning (below) makes this correspondence not surprising, and the two extant reports of the masses of ballooning spiders (from sites in the USA and Australia: Greenstone et al. 1987; a subset analyzed further in Coyle et al. 1985) show a strong bias toward small size. Two other studies, in which body length but not mass was measured, reported comparable size profiles (Dean & Sterling 1985; Bishop 1990). The bias toward small size is also reflected by the small proportion of adult spiders in the aeronaut fauna in all taxa but those in which adults themselves are quite small (Meijer 1977; Dean & Sterling 1985; Greenstone et al. 1987; Bishop 1990).

Because of size differences among spider species, the aeronaut fauna is not a random subset of the communities from which it was drawn, and other differences make the aero-

naut population diverge still further from the source community. For some species, the population of aerially dispersing individuals is strongly correlated with the population density of the source community (Weyman et al. 1995). For others, however, both evolutionary history and local ecological conditions can be influential: Richter (1970) and Greenstone (1982) found that wolf spiders that had evolved under conditions of habitat abundance and predictability (respectively) were less disposed to aerial dispersal than were wolf spiders for which habitat scarcity and unpredictability characterized their evolutionary history; and van Wingerden and Morse showed that the decision to emigrate via ballooning was strongly influenced by the immediate physical environment (in immature linyphiids, van Wingerden 1980) and by foraging prospects in the immediate vicinity (in immature thomisids, Morse 1993).

We can conclude from the studies cited above that the population of airborne spiders is taxonomically rich, composed of physically small individuals, and not a representative sample of the ground-based community. But we know very little about how the population changes seasonally relative to the source community (Weyman et al. 1995) or how it changes latitudinally (Greenstone et al. 1987), and the range of ecologically and geographically different sites from which our knowledge is drawn is very narrow.

Population and distribution effects.—Ballooning spiders are undoubtedly influential

in shaping population structure during the colonization of newly opened habitat (Meijer 1977; Edwards 1988; Thornton et al. 1988; Bishop & Riechert 1990). It is possible that ballooning plays an important role in the colonization of remote islands and in major extensions of a species' distribution (McCook 1878): the occurrence of airborne spiders at high altitudes (Glick 1939; Gertsch 1979) and scores of km from the nearest land mass (Darwin 1839; Hardy & Cheng 1986) suggests that ballooning could indeed be important in these roles, but Platnick (1976) has argued against that suggestion on probabilistic as well as logical grounds.

At a more regional scale, recent studies of spatial dynamics in model agroecosystems indicate that ballooning can substantially modify well-established communities both through aerial dispersal and through aerial deposition (Halley et al. 1996; Thomas 1996; Thomas et al. in press). The literature, however, does not yet allow us to assess the net effects of ballooning (deposition minus dispersal; Weyman & Jepson 1994) in either natural or agricultural settings, nor does it allow an evaluation of the relative roles of aerial and terrestrial migration (Thomas et al. 1990).

And finally at a very local scale, I know of only one study in which actual horizontal distances during dispersal have been measured: Morse (1993) determined that, for the 20 hatchling thomisids he was able to observe from beginning to end of aerial dispersal episodes, the mean horizontal distance covered was 2.7 ± 2.3 m (S.D.).

Meteorological conditions.—Spiders that are inclined to disperse via ballooning can do so only when micrometeorological conditions permit and, in particular, when there is a substantial vertical component in the movement of the air (see below). Several authors have investigated the relationships between these conditions (at a variety of scales) and the numbers of airborne spiders: Vugts & van Wingerden (1976) observed that high numbers of ballooning spiders occurred when the ratio of buoyancy-produced turbulence to shear-produced turbulence was high, a condition characteristic of sunny days with light winds (Humphrey 1987); Greenstone (1990) identified mean wind speed less than 3.0 m/sec and a strong vertical gradient in horizontal wind speed as important in the process, but could

not reconcile his results with the expectation that weather conducive to the production of thermals would be important; and Bishop (1990) found that air temperature in the fall and dew point temperature in the spring were negatively correlated with the abundance of airborne spiders. Although the absence of a consensus among (and within) these studies regarding the meteorological variables that are most important in predicting aeronautical behavior probably reflects the complexity of atmospheric processes (Geiger 1965; Panofsky & Dutton 1984; Anderson et al. 1986), it may also reflect the related problem of scale: in Greenstone's study (1990), meteorological data were collected 5 km and 11 km away from the sites where ballooning spiders were collected; in Vugts & van Wingerden's study (1976), meteorological data were collected from a few meters to 3 km from the sites of ballooning; and in Bishop's study (1990), meteorological measurements were made a few meters from spider collection traps.

Despite the disunity about meteorological parameters of primary importance, there is agreement that ballooning is most common during daylight hours, when wind speed is < 3 m/sec, and under clear skies (Duffey 1956; Richter 1970, 1971; van Wingerden & Vugts 1974; Yeargen 1975; Vugts & van Wingerden 1976; Tolbert 1977; Greenstone 1982, 1990; Bishop 1990).

Behavior and physics.—A spider attempting to become airborne first climbs to the top of some blade of grass, twig, flower head, or fence post, and then either adopts a "tiptoe" stance and emits silk into rising airstreams or drops on a dragline and emits ballooning silk once suspended (Tolbert 1977; Gertsch 1979): either behavior serves to insert both the spider and its silk into moving air. At some point, when the vertical component of the air's motion generates enough drag to counteract the pull of gravity on the spider and its silk, the spider releases its hold on the substrate (structure or dragline) and becomes airborne.

The efficacy of the take-off initiating behaviors and the ability of a spider to remain airborne depend fundamentally on the physics of the interaction between moving air and the spider with its silk. Humphrey (1987) was the first to elucidate the physics on which ballooning depends, and his paper remains at the core of our understanding of the fluid dynam-

ics underlying ballooning. Two subsequent studies, both empirical investigations of drag on spiders and their silk (Suter 1991, 1992), have sharpened the picture somewhat. As a result of these three studies, we now know (1) that only very small spiders can rely on ballooning for dispersal over large distances, (2) that both silk and the spider itself (especially the legs) provide the drag necessary to become airborne, and (3) that the spider has both postural and silk-length control over the magnitude of the drag forces. We also have both theoretical (Humphrey 1987) and empirical (Suter 1991) equations describing the relationships among silk length, spider mass, drag, and terminal velocity.

The details of the behaviors that allow ballooning, particularly with respect to the first steps in the production of the ballooning silk (Eberhard 1987) and the timing of the decision to let go of the substrate, remain obscure. We also know almost nothing about the actual lengths of silk used by spiders during ballooning and so are constrained in evaluations (Henschel et al. 1995) of surprising assertions that very large spiders sometimes disperse by ballooning (Wickler & Seibt 1986).

I have identified several gaps in the ballooning literature and propose, with this paper, to begin filling one of them. In the region where behavior and physics interact, I hope to answer the following question: What expectation can an aerially dispersing spider have regarding its immediate future?

METHODS

I monitored insolation, total wind speed, and the vertical component of air movement in an old field in Dutchess County, New York, in September 1997. The vegetation in the field was dominated by goldenrod (*Solidago* sp.) which had recently finished blooming and by unidentified (and much shorter) grasses. The top of the goldenrod canopy varied from 1.2–1.4 m in height.

To visualize the flow of air in the 0.4 m just above the goldenrod canopy, I used an array of four smoke streams, each emanating from the tip of a stainless steel tube (outside diameter = 1.8 mm). The smoke, produced at the tip of each tube by the interaction of TiCl_4 with atmospheric water to produce TiO_2 , provided a dense white plume that I photographed against the relatively dark back-

ground of distant trees. Each steel tube, rising vertically from the level of the canopy, was 10 cm cross-wind from its nearest neighbor, and the tops of the tubes were at 0, 15, 30, and 45 cm above the canopy. The slender outside diameter of the tubes ensured that they would only minimally affect the downwind structure of the atmosphere, and their placement ensured that they would not influence each other.

Because I wanted to be able to measure meteorological conditions in the immediate vicinity of a ballooning initiation site, I designed a sensor array on which the maximum distance between sensors was 8 cm and from which I could collect data digitally at a relatively high rate. The array consisted of (1) the probe to an omnidirectional hot-wire anemometer (5 mm diameter probe mounted so that the sensitive element was its highest point: Thermonetics Corporation model HWA-103), (2) a force transducer measuring only the vertical component of air motion (a galvanometer-based force transducer described elsewhere [Suter 1992] in which the responsive element was a horizontally mounted square of clear polyethylene, 1 cm \times 1 cm, that was free to move only in the vertical plane), and (3) a UV-sensitive photodiode filtered to remove > 99% of visible light. The vertical force transducer (2) was calibrated against the hot-wire anemometer (1) in a low-velocity wind tunnel prior to the collection of field data. The array was attached to the top of a tripod and adjusted so that the sensor array was at the level of, and surrounded by but not touching, the tops of nearby inflorescences making up the canopy of *Solidago* sp. Prior to collecting data, the array was rotated so that an imaginary line connecting the two air velocity sensors would be perpendicular to the predominant wind direction and the light sensor was downwind from both.

Analog signals from the sensor array were digitized by an analog-to-digital (A/D) converter (National Instruments Corporation model NB-MIO-16L) driven by a custom program (National Instruments software LabView 3) on a microcomputer (Apple Corporation model Power Macintosh 7100/80AV) located 5 m cross-wind from the sensor array. The software handled calibration, converted the signals into units of velocity (m/sec) and insolation (arbitrary units of intensity), and

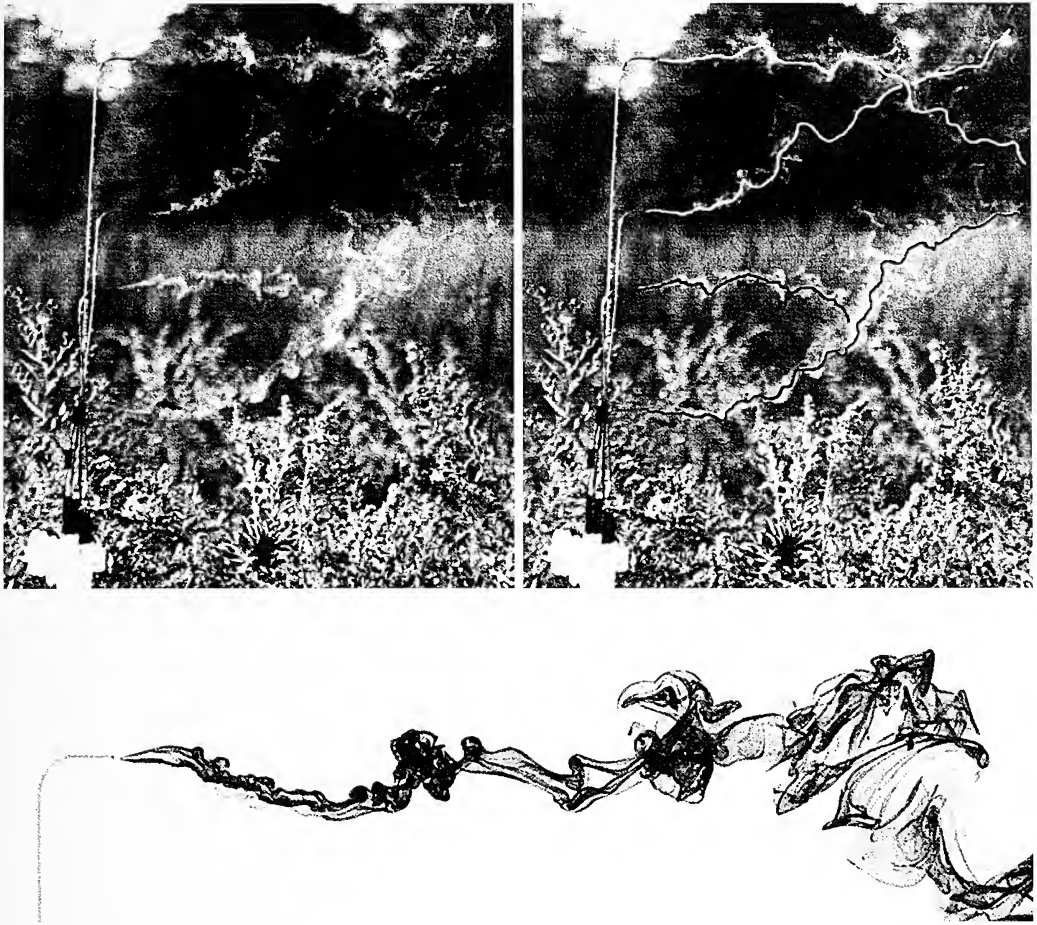


Figure 1.—Titanium dioxide (TiO_2) smoke streams elucidate the turbulent structure of moving air just above the goldenrod canopy. The four smoke streams (top left; unmodified photograph), originating at 10 cm intervals horizontally and at 15 cm intervals vertically, indicate that even small cross-wind displacements result in large differences in flow patterns, even to the extent that one smoke stream may rise while its nearest neighbor falls (top right; hand tracings of plumes added to enhance clarity). A negative image of one plume (bottom), photographed during a period of roughly horizontal air flow, indicates that even at quite small scales air movement appears to be turbulent. In each image, the length of the horizontal portion of the smoke tubing is 3 cm.

stored the data to disk. Trios of data were recorded at 0.1 Hz, resulting in accumulations of 360 trios of data per hour and 4320 trios per 12 hour day. Given the variability inherent in a turbulent atmosphere at all scales (Schlichting 1979), this rate of data collection must underestimate the total atmospheric variability (see results).

RESULTS

I collected data on three days during which I also observed ballooning (by unidentified spiders) from *Solidago* inflorescences at the study site. Photographic images (Fig. 1) of

smoke plumes during this period indicated, at least qualitatively, that air movement just above the goldenrod canopy was remarkably variable at several scales. I report here quantitative data and analyses based on only one of the sample days (15 September 1997) primarily because data from the three days were very similar. Raw data for the subject day show that the sun was visible throughout the day with the exception of brief intervals when small clouds obscured it, that wind velocity varied from 0–2.5 m/ sec, and that the vertical component of air movement was generally upward prior to 1300 h and downward during

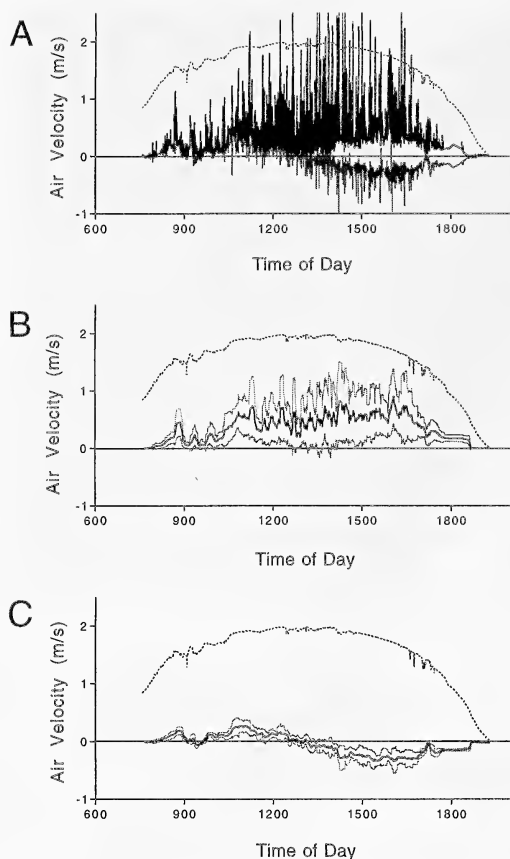


Figure 2.—(A) Raw data for 15 September 1997 depicting insolation (dotted line), total wind velocity (black line), and the vertical component of air movement (gray line) at the top of a canopy of *Solidago* sp. (B) Mean wind speed (black line, 30-point running average) \pm S.D. (gray lines) derived from the raw data. (C) Mean \pm S.D. values for the vertical component of air movement. Brief downward displacements of the insolation line represent periods when the sun was partly or entirely obscured by small clouds. The change from upward to downward air motion at approximately 1300 h (A & C) provided the rationale for later analytical emphasis on the period prior to 1300 h.

the remainder of the day (Fig. 2A). Thirty-point running averages \pm S.D. for total wind velocity (Fig. 2B) show that average wind velocity was < 1.0 m/sec throughout the day, and similarly processed data for the vertical component of air movement (Fig. 2C) emphasize the difference between pre-1300 h and post-1300 h conditions.

A sample-by-sample trigonometric combination of total wind velocity with the vertical component of air motion yielded both the in-

clinations (negative indicates an upward inclination, in keeping with the biological convention in which geotaxis is positive when toward the earth) and the magnitudes of the resultant air motion vectors (Fig. 3A). Because ballooning could occur only rarely after 1300 h, those data are ignored in the analyses that follow. The velocity vector magnitudes for pre-1300 h are distributed approximately log-normally (Fig. 3B) as -0.93 ± -0.77 (\log_{10} m/sec; equivalent of 0.117 ± 0.170 m/sec, mean velocity \pm S.D.; $r^2 = 0.93$), although the idealized distribution overestimates very low velocities and underestimates velocities between 0.2 and 0.5 m/sec. The velocity vector inclinations for pre-1300 h are distributed approximately as a circular normal distribution (Fig. 3C; Batschelet 1981) with an upward-directed mean of $-19^\circ \pm 27^\circ$ (mean \pm angular deviation, mean vector loading, $r = 0.885$; $r^2 = 0.87$). A linear regression of inclination on magnitude for the pre-1300 h data had a significantly positive slope ($r^2 = 0.022$, $F = 19.58$, $P = 0.0001$), indicating a slight tendency ($\sim 2\%$ of the variance explained) for the inclination to become more downward as magnitude increased (negative values indicate upward inclination).

The chaotic character of the turbulent atmosphere at the canopy of a field means that, from moment to moment at a single location, air velocities and directions are apparently random (Panofsky & Dutton 1984; and note ratios of mean to S.D. for both velocities and inclinations, above). This apparent randomness allows one to treat frequency distributions as probability functions. Accordingly, a surface that shows the probabilistic structure of air motions at the sensor array, in terms of magnitude (Fig. 3B) and inclination (Fig. 3C), can be constructed as the product of the inclination and magnitude frequency distributions (Figs. 4A and 4B). Note that, because of the relatively low sampling rate (0.1 Hz) used in the collection of the data from which these analyses were derived, and the consequent underestimation of the variability in atmospheric motion at small scales, the calculated probabilities (Figs. 4–6) are overestimates of the true probabilities experienced by ballooning spiders.

An exploration of this unpredictable but statistically defined situation for spiderlings of known sizes is instructive. The terminal ve-

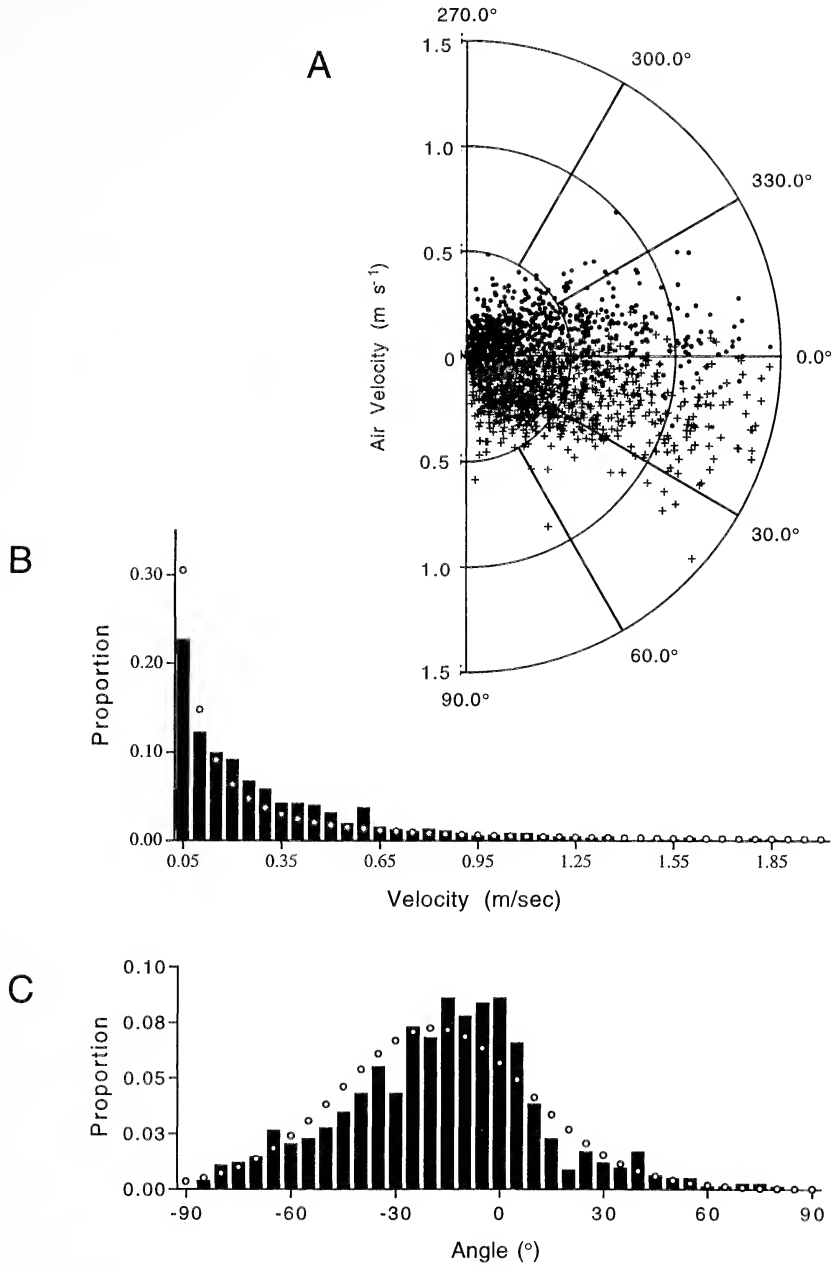


Figure 3.—(A) Trigonometric calculations based on air movement data (Fig. 2A) resolved the data into its vector components (magnitude and inclination). Pre-1300 h data (filled circles) are used in subsequent analyses to the exclusion of the post-1300 h data (crosses). (B) In the pre-1300 h data, air movement magnitudes (bars) were approximately log-normally distributed (open circles) with a mean of -0.93 log units (0.117 m/sec). (C) The inclinations of the pre-1300 h data (bars; negative angles are upward) formed an approximately circular normal distribution (open circles) with a mean direction of -19° and angular deviation of 27.1° .

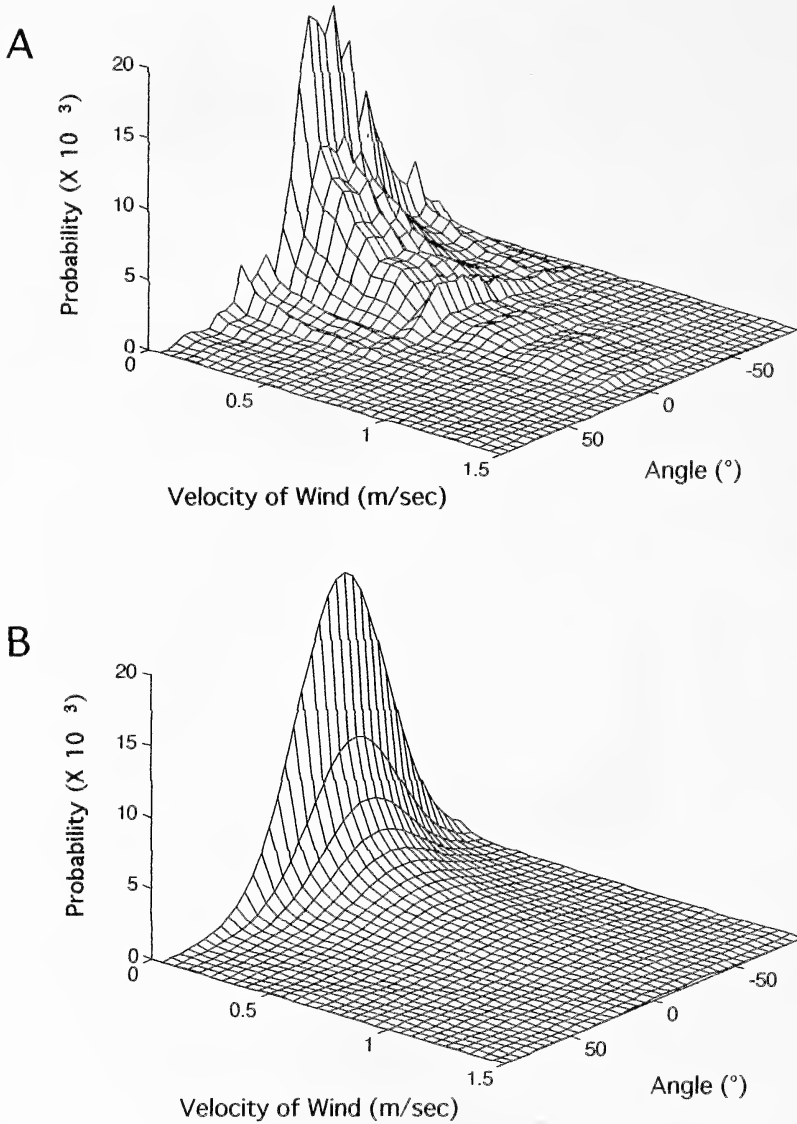


Figure 4.—Probability distributions derived from the data in Fig. 3 for (A) the actual data distributions and (B) the idealized (log-normal and circular normal) distributions.

locity of a 0.4 mg spider trailing 1 m of silk is about 0.24 m/sec (Equation 7 in Suter 1991) if both its body and its silk are in the same column of air. The vertical component of air velocity (speed·sin(inclination angle)) must then exceed 0.24 m/sec if the spider is to become, and remain, airborne. (Because the spider standing in the “tiptoe” posture at the top of a plant is in air moving more slowly than the air surrounding the silk, this estimate of minimum vertical magnitude is an underestimate for becoming airborne; Suter 1991.) The part of the angle-velocity plane shown in Fig.

4B that meets the criterion of having the vertical component of wind velocity > 0.24 m/sec is quite limited (Fig. 5). The sum of all probabilities in the elevated part of the surface (Fig. 5, 0.4 mg), P , is 0.101. Thus the 0.4 mg spiderling, at any moment, has $P \leq 0.1$ that in the next 10 sec conditions will be momentarily suitable for becoming airborne, and the probability that those conditions will persist for 20 seconds is $P^2 \leq 0.01$. This analysis is sensitive both to the mass of the spider and to the length of silk in use as a “balloon.” A spider of twice the mass,

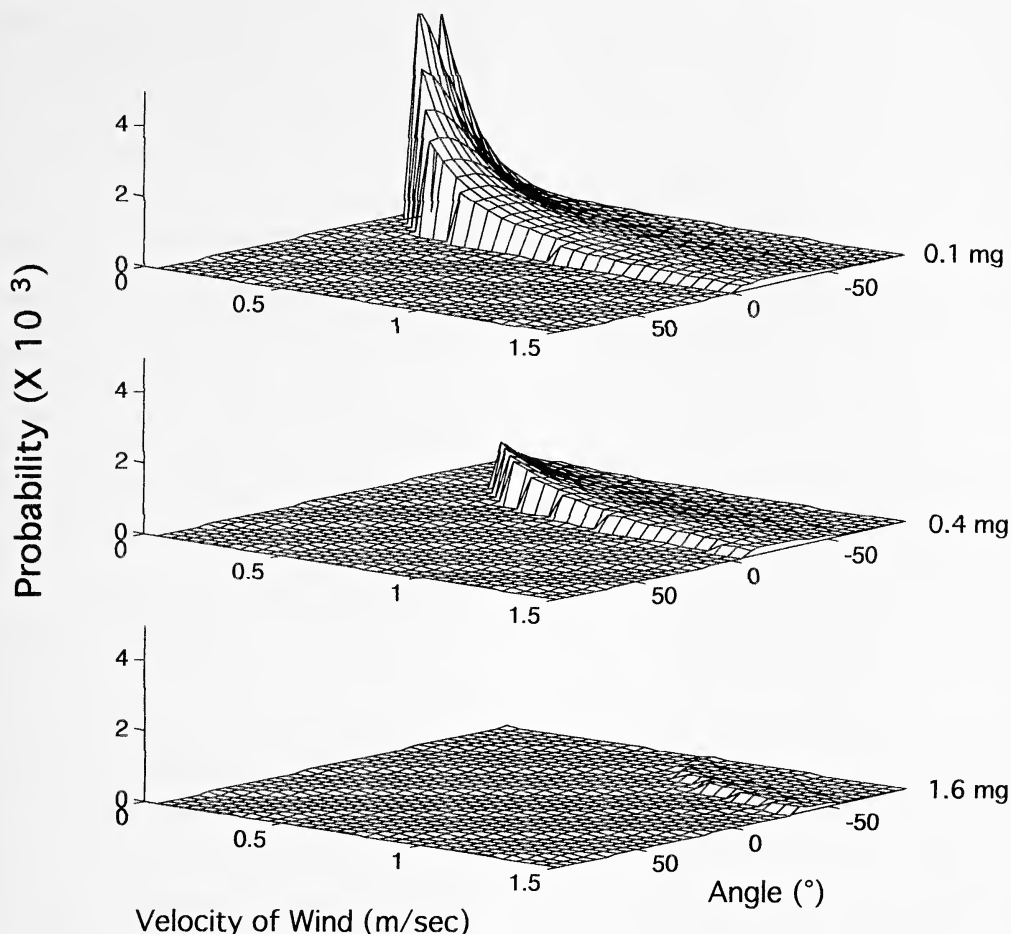


Figure 5.—A spider can become airborne only if the upward component of the air velocity vector exceeds the terminal velocity of the spider with its silken “balloon.” For a 0.1 mg spider with a 1 m length silk (top), the probability of becoming airborne in any 10-sec period is the volume under the elevated part of the surface, about 0.28. The probability falls steeply with increasing mass, so that a 1.6 mg spider has a probability near zero for the conditions that prevailed during the pre-1300 h period of 15 September 1997.

using the same 1 m of silk, would have a terminal velocity of 0.43 m/sec, would encounter sufficient vertical air movement at $P \leq 0.044$, and could count on 20 s of those conditions at $P^2 \leq 0.002$. In terms of probabilities, smaller spiders attempting to balloon have disproportionately greater access to aerial dispersal than do larger spiders (Fig. 6A). The release of additional silk, a behavioral tactic, also influences P but the effectiveness of increases in silk length decline with length (Fig. 6B).

DISCUSSION

A spider attempting to balloon from the highest point on a plant is bathed in air the

motion of which is demonstrably unpredictable (Fig. 2A), chaotic (Panofsky & Dutton 1984), and best described probabilistically (Figs. 3–6). Thus the spider’s perception of the current state of its microclimate, at least with respect to air direction and speed, has almost no predictive value and cannot contribute, except in a statistical sense, to the spider’s decision-making.

Behavioral consequences.—Faced with the stochastic atmospheric environment imposed by turbulence in the air surrounding a ballooning site, what tactics can a would-be aeronaut adopt to maximize its probability of success? (1) Because favorable micro-scale

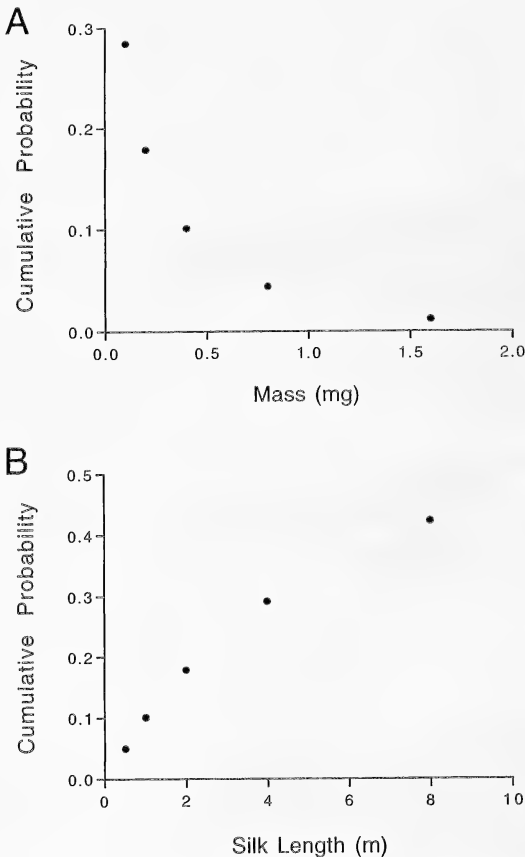


Figure 6.—The cumulative probability of becoming airborne (A) decreases strongly with increasing mass (at a constant silk length of 1 m) and (B) increases with the length of the balloon silk (for a spider of mass 0.4 gm). The mass relationship provides a partial explanation for the data on the masses of actual aeronauts (see references) and suggests a developmentally coupled decay in a spider's proclivity for ballooning. The silk-length relationship, in contrast, indicates that a spider can have some behavioral control over the probability of becoming and remaining aloft.

conditions rarely persist for more than a few seconds, the spider should deploy silk rapidly and release from the substrate as soon as some vertical acceleration is assured (a testable prediction because p is an inverse function of mass [Fig. 6A], so that silk deployment rate should increase with mass and latency to release should decrease with mass). Put another way, a 0.2 mg spider can more easily afford to wait for improved conditions than can a 0.4 mg spider, but both should be relatively responsive to marginal conditions. (2) Because

post-release posture strongly influences drag (Suter 1992), the spider should assume a spread-eagle posture (all unoccupied legs extended) immediately upon release, a tactic more important for larger spiders because of their increased terminal velocities. This behavior would also be beneficial if air flow were laminar (which it never is at the canopy), but its importance under turbulence is increased because favorable conditions are so transitory. Finally, (3) spiders climbing toward a site from which to balloon should be selective if their sensory capabilities permit: the rarity of conditions (i.e., high magnitude and inclination) that could rapidly extract a ballooning spider from the vicinity of obstacles favors selection of the highest local promontory, and again, selectivity should be most evident in larger spiders.

Consequences for larger spiders.—Fluid dynamic calculations (Humphrey 1987; Suter 1991) make clear that ballooning is a dispersal mechanism that is primarily available to small spiders. The bias against large ballooners is strengthened by other considerations as well: climbing is more energetically expensive for large than for small spiders (Thompson 1942; Price 1984), and large spiders, given their higher terminal velocities, have to climb more frequently than small ones to achieve the same horizontal displacement; larger spiders are more conspicuous to predators; and favorable conditions under turbulent conditions vanish rapidly as spider size rises (Fig. 6A). It is not surprising, therefore, that this pronounced bias is mirrored in data on the sizes of aeronauts (Dean & Sterling 1985; Greenstone et al. 1987; Bishop 1990).

Complications.—In this paper I have analyzed micrometeorological data from a single day and, had I chosen another day, the data would surely have been different in detail. But ballooning did occur during the morning of the subject day, the day was similar to those described by others as prime for ballooning (Vugts & Van Wingerden 1976), and the characteristics of turbulent flow over a single habitat within a specific range of velocities (e.g., 0–3 m/sec) are remarkably consistent (Panofsky & Dutton 1984; Anderson et al. 1986). More problematic is the consideration of only a single site within the field—other sites, being closer to a tree line or hedgerow or more remote from a patch of field dominated by low

grasses, could have quite different atmospheric characteristics. A study of site-specific aerodynamics, and particularly the identification of features (such as down-wind barriers) that cause consistent and stable updrafts, is certainly warranted.

Much of the analysis used in this study has been statistical and probabilistic rather than strictly mathematical. This is a necessary consequence of the structure of a turbulent atmosphere and its chaotic (and apparently random) behavior as it moves past a fixed point from which a spider might attempt to balloon. From the perspective of an airborne spider, the situation is equally complex but very different because the spider and its silk are now incompletely entrained in air that is characterized by eddies of many sizes (e.g., Gao et al. 1989) that are relatively coherent as they move downwind (Zhang et al. 1992). A full understanding of the motion of airborne spiders in the turbulent air above agroecosystems is still a long way off.

Finally, during a particular ballooning attempt, the risk of failure (going only a short distance horizontally) is high (Fig. 3), but that kind of risk is relatively cost-free for very small spiders: returning to an exposed tip of a plant, even repeatedly, is energetically cheap (Thompson 1942), whereas the risk of predation during a cursorial or drop-and-swing (Barth et al. 1991) dispersal of the same horizontal distance must be considerably greater.

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DIFFERENTIAL AERIAL DISPERSAL OF LINYPHIID SPIDERS FROM A GRASS AND A CEREAL FIELD

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ABSTRACT. Ground and aerial populations of linyphiid spiders were sampled in and above a grass and a cereal field, weekly from June–August 1991. Aerial activity of immature, adult male and adult female spiders was significantly higher over the senescing cereal field than the grass field. Water-trap catches and wind-speed data were used to calculate indices of aerial activity to show differences in the timing of dispersal by adult male, female and immature spiders. Some aerial dispersal occurred every week with highest adult dispersal in July and highest immature dispersal in August. Aerial activity indices were higher for males than females, and the dispersal peak occurred earlier for males than females. Immatures dispersed from the cereal field in July and August, and from the grass field mainly in August. Differences in aerial activity are discussed with reference to dispersal strategies that might maximize spider survival in the patchy, disturbed agricultural landscape.

Several species of linyphiid spider are widespread and abundant natural predators of pests in the agricultural ecosystem (Sunderland et al. 1986). In farmland, the patchwork of annual and perennial crops fragments spider populations into patches of habitat among which resource quality and risks of habitat disturbance vary in space and time. In such spatially structured populations or metapopulations, dispersal behavior is critical for re-founding locally extinct populations (Gilpin & Hanski 1991) and has a major effect on population size and persistence at the landscape scale (Halley et al. 1996).

Little is known of the ancestral habitats of species of linyphiid spider which are now abundant in farmland, or the pattern of disturbance they experienced. Both immature and adult linyphiid spiders are, however, able to disperse over large areas by “ballooning” (Thomas 1996), and this ability is a necessary pre-adaptation for survival in disturbed farmland habitats (Halley et al. 1996). The parameters of dispersal—distance, frequency, timing and the proportion of a population that undergoes dispersal—are all likely to be under

adaptive pressure to maximize survival in agroecosystems by spreading risks or optimizing foraging among the shifting mosaic of available habitats. Throughout history, agricultural fields have been periodically disturbed by harvesting and cultivations. The frequency, severity and predictability of such catastrophic events depends on patterns of land use and methods of production. However, in recent decades, insecticides have become an additional hazard to linyphiid spiders. On an evolutionary time-scale, these changes may have been so sudden and widespread that linyphiid spiders are unable to adapt; and there is some evidence that the abundance of linyphiid spiders has been declining in UK arable farmland since the 1970s (Aebischer 1990).

In order to understand linyphiid spider responses to changing agricultural practices and patterns of land use, a simulation model of spatially dynamic spider populations has been developed (Halley et al. 1996). All the dispersal parameters mentioned above can be varied in the model. However, in that model, the dispersal process is simplified such that the proportion of dispersers in the population is the same across all habitats. Other parameters apply equally to both sexes and all age classes. This decision was based on the assumption that meteorological factors were the most important constraint on dispersal, affecting all spiders uniformly. The critical constraint is wind-speed which must be below 3

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ms^{-1} for ballooning to occur (Vugts & van Wingerden 1976). However, the model has shown that small differences in the duration and timing of dispersal can have large impacts on population size and persistence (Halley et al. 1996; Thomas 1997).

Wind tunnel studies have shown that approximately 40% of linyphiid spiders attempt to balloon when wind conditions are suitable (Legel & van Wingerden 1980). Computer simulations have also shown 40% to be the optimum dispersal rate that maximizes population size in a wide range of agricultural landscapes (Halley et al. 1996). Age or sex specific differences in the proclivity to disperse from different crop types under the same meteorological conditions may, therefore, result in different risks to different sections of the population; and these aspects require further investigation.

This paper describes field observations on the aerial activity of male, female and immature linyphiid spiders dispersing from known populations in a cereal and a grass field. The results are discussed in terms of possible differences in the relative importance of dispersal in foraging and risk-spreading strategies thought to be relevant to each group.

METHODS

In June, July and August 1991, during the most active phase of summer reproduction and dispersal, linyphiid spiders were sampled at weekly intervals from a winter wheat field and a grass field. Eleven samples, totaling 5.28 m^2 , were taken from near the center of each field with a suction sampler (D-vac), each consisting of five sub-samples of a 10–15 second application of the suction head (0.096 m^2) to the soil surface enclosing any foliage present in a net 1.5 m long.

Over the same period, aerial activity was measured with two water traps in each field. Traps were constructed from square, galvanized steel trays 1.2 m on each side and supported on a metal frame one meter above the soil. Eight plastic seed trays ($46 \text{ cm} \times 27 \text{ cm}$, Stewart Plastics, UK) were placed within the steel tray. The inner trays were filled with 50% ethylene glycol in water containing 2.5% detergent and had a total surface capture area of 1 m^2 . The outer steel tray was also filled with water and detergent to prevent access to the inner trays by spiders climbing in from the

crop. The inner trays thus trapped only ballooning spiders landing from the air, giving a measure of aerial dispersal activity. Parallel studies on the change of spider aerial density with height (Thomas 1992) indicated that the water trap catches were dominated by spiders from low altitudes attempting to disperse from the field in which the trap was situated. Spiders descending from higher altitudes, having dispersed from more distant fields, are likely to form only a small proportion of the trap catch. Water traps were emptied at weekly intervals by sieving the contents through a fine nylon mesh of the same material as the D-vac net. Samples were sorted in the laboratory under a dissecting microscope, and adult linyphiid spiders were sexed and identified to species. Because immature spiders could not be identified to species, data are presented for all species combined.

Because aerial dispersal does not occur when wind-speeds are greater than 3 ms^{-1} (Vugts & van Wingerden 1976) an anemometer (Lambrecht, Germany) was used to record wind-speed on paper chart to quantify the amount of time suitable for dispersal during each sampling period. This was defined as the total number of hours between 0600–1800 h GMT with wind-speeds below the 3 ms^{-1} ballooning threshold. In each trapping period, the total water trap catch was converted to an aerial activity index, expressed as the total number of spiders trapped in each field, per hour of available ballooning time.

RESULTS

Linyphiid spiders comprised more than 95% of the sampled population. Other families were not considered in this study. The samples were dominated by five taxa: *Erigone atra* (Blackwall), *E. dentipalpis* (Wider), *Meioneta rurestris* (C.L.Koch), *Lepthyphantes tenuis* (Blackwall) and *Oedothorax* spp. A sixth taxon “other species” comprised a few individuals of a number of species. An earlier study (Thomas & Jepson 1997) showed no significant difference between the species composition of water trap samples and D-vac samples (Fig. 1). Data are therefore presented as total linyphiids, divided into the categories “immature,” “adult male” and “adult female”.

Table 1 shows the total numbers of immature, adult male and adult female linyphiid

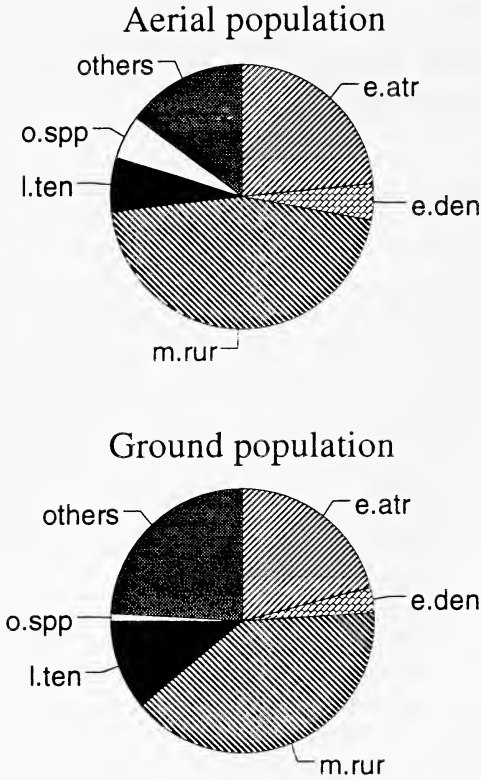


Figure 1.—Percentage population composition of dominant taxa from suction samples (total ground population) and water trap samples (total aerial population) based on data from a previous study (Thomas & Jepson 1997) at the same field site. Abbreviations: e.atr = *Erigone atra*; e.den = *E. dentipalpis*; m.rur = *Meioneta rurestris*; l.ten = *Lepthyphantes tenuis*; o.spp = *Oedothorax* spp.; others = other linyphiid species.

spiders, captured in the water traps and sampled on the ground in the two fields. Significant differences between captures in the grass and cereal field on each date, tested by χ^2 , and the total number of available hours for ballooning are also given. Aerial activity indices (number of trapped spiders divided by number of hours available for ballooning during trapping period) for immature, adult male and adult female spiders, in the grass and cereal fields, are given in Fig. 2.

During June and early July aerial dispersal was too low on some dates to test for significant differences between numbers of spiders captured in the grass and cereal field, either on the ground or from the air (Table 1). In mid-July there were significantly more immature spiders captured over the cereal crop

when the population density on the ground was significantly higher in the grass field than the cereal field. In August, there were significantly more immature spiders from the grass field compared to the cereal field, in both aerial and ground samples. A 2×2 contingency test on total raw counts of air and ground samples from the grass and cereal field, over the entire experimental period, was highly significant by *G*-test using Williams' correction (Sokal & Rohlf 1981): $G_{adj} = 871.5$; $df = 1$; $P < 0.001$, indicating a significantly higher proportion of captures of airborne immature spiders over the cereal crop than expected from the respective ground population densities in the two fields.

During late July and August, there were significantly higher numbers of adult males and females caught in the water traps in the cereal field, compared with the grass field. Between early June and mid-July, there were significantly higher ground population densities of adult males and females in the cereal field compared to the grass field, or no significant difference between the two populations. After the end of July and during August, following a week with the highest number of ballooning hours (week ending 3 August: 69 hours of wind-speed below 3ms^{-1}) the pattern reversed; and there were significantly higher ground population densities of adult males and females in the grass field compared with the cereal field, suggesting a net emigration from the cereal field and a net immigration into the grass field. A 2×2 contingency test on total raw counts of air and ground samples from the grass and cereal field over the entire experimental period was highly significant by *G*-test for both male ($G_{adj} = 37.0$; $df = 1$; $P < 0.001$) and female spiders ($G_{adj} = 32.4$; $df = 1$; $P < 0.001$). As for the immature spiders, these results indicate that higher proportions of adult male and female airborne spiders were taken over the cereal crop than expected from the relative ground population densities in the grass and cereal field.

Figure 2 shows the water trap catches in each week divided by the number of hours of available ballooning time. In both the grass and cereal fields, there was little ballooning activity up to July 3. Thereafter, the majority of dispersal by male spiders occurred over a period of three weeks, with a peak occurring during the week ending July 18. On each date,

Table 1.—Aerial and ground captures of linyphiid spiders in a grass and cereal field. Significant differences tested by chi square. $P < 0.05 = *$; $P < 0.01 = **$; $P < 0.001 = ***$; ns = not significant. Dates with expected captures < 5 not tested.

Sample period week ending (ballooning hours)	Immatures		Adult males		Adult females	
	Grass	Cereal	Grass	Cereal	Grass	Cereal
Aerial activity (spiders/trapping period)						
4 June (8)	22	9*	4	2 —	1	2 —
13 June (20)	8	20*	1	1 —	1	1 —
18 June (7)	1	3 —	1	0 —	0	0 —
25 June (6)	3	2 —	2	1 —	0	0 —
3 July (32)	3	5 —	12	2**	8	1 —
9 July (7)	2	16***	47	54ns	16	16ns
18 July (10)	12	46***	112	159***	20	92***
25 July (14)	49	64ns	79	110*	65	157***
3 August (69)	506	291***	72	114***	110	53**
10 August (19)	585	270***	20	38*	38	39ns
17 August (24)	809	521***	41	38ns	58	44ns
Ground population density (spiders/5.28 sq m)						
4 June	82	27***	1	8 —	0	4 —
11 June	59	36*	0	11***	2	14**
18 June	105	104ns	11	15ns	3	23***
26 June	148	158ns	32	39ns	26	27ns
4 July	136	88**	95	90ns	76	58ns
9 July	60	54ns	132	109ns	77	69ns
16 July	153	84***	72	85ns	61	80ns
23 July	759	128***	59	122***	48	160***
30 July	2316	98***	177	43***	154	62***
6 August	3454	667***	115	65***	96	87ns
13 August	3335	289***	117	55***	172	103***

higher numbers were trapped over the cereal field than the grass field. Female spiders also showed increased dispersal during this period, although this was generally lower than the males and the dispersal peak occurred one week later. The aerial activity indices of females were generally much higher over the cereal field than the grass field. Immature spiders had higher aerial activity indices over the grass field in August, reflecting the higher population densities on the ground in that field. However, immatures began to disperse from the cereal field earlier than from the grass field.

DISCUSSION

The D-vac and water traps are not 100% efficient sampling devices. However, they are the most reliable and cost-efficient methods available. The water traps are of comparable efficiency, regardless of where they are sited. The efficiency of the D-vac, however, is de-

pendent on the vegetation structure and density (Duffey 1980). In this study, the populations sampled from the dense grass sward are likely to have been underestimated in comparison with the populations in the much less dense stand of cereal. Thus, where the densities of linyphiid spiders in the grass field are shown to be higher than the cereal field (Table 1), the true differences are likely to have been even greater.

Although water traps can be left unattended in the field where they catch dispersing spiders effectively, the number of spiders they trap is not directly related to the number of spiders ballooning. A ballooning spider takes off and lands a number of times during a dispersal episode, dependent on the amount of atmospheric turbulence on a given day (Thomas 1992). Thus, water trap catches are a function of the size of the source population on the ground, the proportion of the population that engages in dispersal, the number of

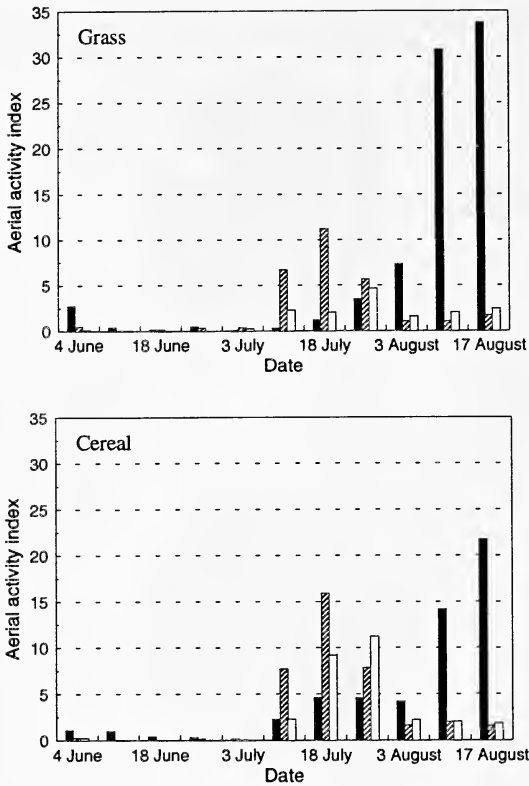


Figure 2.—Aerial activity indices expressed as the total number of spiders in water traps per hour of available ballooning time (wind-speed < 3ms⁻¹) for immature (filled bars), adult male (hatched bars) and adult female (open bars) spiders in a grass field (top), and a cereal field (bottom).

hours of available ballooning time, and the take-off and landing rates on different days during a trapping period, which might comprise several ballooning episodes. Quantitative estimates of differential dispersal rates from different habitats, therefore, can only be obtained by simultaneously measuring the numbers of spiders initiating dispersal behavior from given areas of ground in different crops and relating these to the respective ground population densities over the same area.

In spite of the limitations of the sampling methods employed, there is good evidence that dispersal from senescing cereal fields by linyphiid spiders is significantly higher than from grass fields. Similar results have been demonstrated by Weyman et al. (1995). There are also good theoretical reasons why differential dispersal should be expected. Cereal and grass fields provide different quality hab-

itat, especially in the late summer when perennial grass, if left uncut, provides a cool, humid microclimate, while senescing annual cereals provide a hot, dry microclimate (Geiger et al. 1995). These micro-climatic differences, and the different resources provided by a lush perennial and a senescing annual crop, are also reflected in the fauna sampled with the spiders from the two habitats. In the grass field, high prey density (mostly Collembola, aphids and Diptera) was found while in the cereal field, low prey density was found (pers. obs.). Further evidence of differences in habitat quality between the grass and the senescing cereal field comes from the observation of significantly higher production of immature linyphiid spiders in the grass field compared with the cereal field (Table 1). These factors are likely to affect the level of satiation of spiders, which is known to affect their propensity to disperse (Legel & van Wingerden 1980; Weyman et al. 1994). Linyphiid spiders have also been shown to be retained in experimental plots with high prey density (Weyman & Jepson 1995), presumably by reduced emigration.

A number of dispersal strategies may operate in this system and be adopted to different degrees by different sections of the population. When suitable meteorological conditions prevail, opportunistic dispersal between habitat patches of differing quality in the farmland mosaic might form the basis of a foraging strategy. When annual crops ripen and senesce, causing gradual deterioration of habitat quality, a resource-assessment strategy (Parker & Stuart 1976) might operate, e.g., spiders may respond to a marginal value (Charnov 1976) of food availability or threshold of environmental stress and initiate dispersal only when this is reached. Some aspects of these behavioral strategies have been reviewed by Janetos (1986) and Riechert & Gillespie (1986).

In agroecosystems where habitat patches have a probability of undergoing unpredictable catastrophic disruptions, e.g., harvesting or insecticide applications, a risk-spreading strategy (den Boer 1968) might operate. The risk to a sedentary spider of succumbing to unpredictable catastrophic events in the habitat patch in which it is resident needs to be balanced against the probabilities of dispersing to a more favorable habitat patch, dis-

persing to a less favorable habitat patch, and the risk of dying during dispersal.

Male and female spiders might also respond differently to the same resources and risks. Adult males feed little when sexually active (Alderweireldt & Lissens 1988) and are therefore partially released from constraints of resource availability. High male dispersal may simply reflect the relative importance of mate-finding over feeding. Females, on the other hand, require more resources for egg production. They may, therefore, be less likely than males to disperse from a high quality habitat where resources and microclimate may also increase the survival of eggs and early immature stages. Some female dispersal from high quality grass fields may still be expected as a strategy to increase overall survival probability of offspring by laying egg sacs in several patches, thus spreading risks among the patchwork of field types in the landscape.

The dispersal strategies of linyphiid spiders in agroecosystems are likely to be complex. More detailed field studies and computer simulations are required in order to resolve the relative importance of different dispersal strategies, predict their effect on the metapopulation dynamics of the group, and determine whether dispersal strategies can adapt fast enough for populations to persist in the face of increased risks associated with insecticide use and other management practices in modern agroecosystems.

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PREY CHOICE AND SPIDER FITNESS

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ABSTRACT. Although spiders in general are polyphagous, indiscriminate feeding is not advantageous because prey vary enormously in quality due to toxicity or nutrient deficiency. Active prey selection serves to find the optimal compromise between three “nutritional goals”: maximize energy intake, balance nutrient composition of the body, and minimize toxin consumption. Consumption of toxic prey is reduced by more or less specific induced aversions, probably associated with both prey taste and behavior. Spiders’ ability to avoid toxic prey seems limited because aversions are short-lasting and some toxic prey do not induce an aversion. Such prey may be lethal. Toxic prey in a mixed diet may inhibit feeding on and utilization of good prey. Induced tolerance to toxic prey may be possible, however. Nutritional balance may be obtained through consumption of high-quality prey or through mixing of prey types. It is argued that nutrient balance is more important than maximization of energy intake for fitness.

Foraging decisions influence individual fitness in a variety of ways. Choice of foraging habitat (patch) has been recognized as being of primary importance through its effect on feeding rates, with derived benefits to growth (size) and reproduction (Riechert 1981; Morse & Stephens 1996). Once in a feeding patch, the spider is confronted with an array of potential prey species. Prey selection is the consumption of prey relative to the composition of prey available in the spider’s microhabitat. So defined, selectivity has two aspects (*cf.* Pastorok 1981; Sih & Moore 1990): 1) passive selection or capture success, and 2) active selection (“choice”), i.e., acceptance/rejection of the prey. Both are clearly important for determining the diet composition in the field. The capture success reflects the co-evolutionary balance between prey and predator in a broad sense (Malcolm 1992) and is largely outside the individual spider’s control. Active selection reflects the spider’s decisions (choices) whether positive (acceptance) or negative (rejection). Spiders are selective if they choose differentially between the prey species according to their preferences. Such preferences by individuals may change over short time spans and, contrary to expectations, they are not necessarily related in a simple way to the nutritional value of the prey (see later). Active and passive selection can be distinguished if prey is presented with and without possibilities for escape (Onkonbury & Formanowicz 1997; Lang & Gsödl unpubl. data).

This review is concerned only with active selection or “prey choice,” and in our own experiments we have confined spiders and prey to small containers. Additionally, I have largely neglected the phenomenon of size selectivity and focus on choice between prey species. Finally, my treatment is biased towards wolf spiders (Lycosidae) and money spiders (Linyphiidae). These two families account for most of the species and individuals of spiders found in agricultural fields of Northern and Central Europe (Sunderland 1987; Nyffeler & Benz 1988a, b; Toft 1989), and most of the studies reviewed were completed with the specified goal of analyzing potentially important trophic links of the agroecosystem. The experimental prey types were likewise selected to represent the most important prey groups as revealed by studies of European cereal fields, i.e., Collembola, Diptera and aphids (Nyffeler & Benz 1988a, b; Sunderland et al. 1986, 1987; Alderweireldt 1994).

Food contains three main components: energy, nutrients, and toxins. Viewed in isolation, feeding behavior should aim at the following three “nutritional goals”: maximize energy intake, balance body nutrient composition, and minimize toxin consumption. They cannot all be realized at the same time. Prey choice is expected to achieve the optimal compromise that maximizes the fitness of the spider.

As spiders are generalist predators, we might *a priori* expect that energy gain would be maximized by accepting all kinds of prey,

i.e., by being non-selective. In line with this, the broad polyphagy of spiders is considered to follow from the prevailing sit-and-wait strategy and a temporally varying food supply (Riechert & Luczak 1982; Riechert & Harp 1987). In the notion of polyphagy it is usually understood that most kinds of potential prey are of approximately equal value to the predator and may substitute each other in the predator's diet (cf. Slansky & Scriber 1985; Waldbauer & Friedman 1991; Wise 1993). Rejection of toxic, dangerous or difficult prey (Riechert & Luczak 1982; Nentwig 1987) as well as novel (unfamiliar) prey (Turnbull 1960; Riechert & Luczak 1982) has, however, been recognized. Prey selection aimed at obtaining a specific composition of amino acids was indicated by Greenstone (1979); but, generally, nutrient balance is considered to be achieved through a mixed diet (Riechert & Harp 1987; Uetz et al. 1992). In conclusion, though the existence of active choice has been acknowledged, most reviews have considered it to be of limited importance.

The questions raised here are: 1) Does active prey choice improve fitness? 2) What mechanisms influence prey choice? 3) Are the three nutritional goals equally important? 4) Do the answers to these questions confirm the inferior role of active selection for spider nutrition?

PREY QUALITY

Prey differ enormously in quality as food for spiders, as indicated by the effects on fitness parameters of keeping spiders on single-species diets (Toft 1995, 1996; Sunderland et al. 1996a, b; Toft & Wise 1999a). Based on laboratory experiments with the wolf spider *Schizocosa* sp., the latter authors establish five quality categories: 1) high-quality prey (e.g., the collembolan *Tomocerus bidentatus*) are nutritionally complete; single-species diets allow complete development (possibly full life cycle); 2) intermediate-quality prey (e.g., laboratory fruit flies *Drosophila melanogaster*) give initially high growth rates, but are insufficient for full development and the spiders die before maturity; 3) low-quality prey (e.g., sciarid midges and conspecifics) allow very little growth and development and spiders die in an early instar; 4) poor-quality prey (e.g., several aphid species) allow neither growth nor development, and performance is no bet-

ter than for starved controls; 5) toxic prey (e.g., the collembolan *Folsomia candida*) result in the spiders dying faster than starved controls. Prey species may have roughly the same quality characteristics for all polyphagous predators, as basically similar results have been obtained for lycosids, linyphiids and carabid beetles (Bilde & Toft 1994, 1997a, b).

With single-species diets no selection is possible. Furthermore, prey species may be insufficient as single prey but make positive contributions to fitness as parts of mixed diets.

DIETARY MIXING

Experiments with mixed diets allow us to analyze the extent to which spiders can choose an optimal diet, given varying prey availabilities. Uetz et al. (1992) demonstrated increased survival and growth rate in *Lycosa* spp. on a mixed diet when compared to a single-prey diet. Toft & Wise (1999a) found the same for *Schizocosa* sp., when fruit-flies and the high-quality collembolan *Tomocerus* were mixed. However, other mixed diets have revealed conflicting results. Thus, performance of *Schizocosa* was below that of the starvation control with two diets mixing two toxic Collembola with higher-quality prey. Toft (1995) found improved reproductive success in the linyphiid spider *Erigone atra* when females were given a mixed diet of fruit-flies and the poor-quality aphid *Rhopalosiphum padi*. From these results it is hypothesized that the positive effect of dietary mixing depends on the quality of the prey species being mixed in the following way: mixing of higher-quality prey may or may not be beneficial; mixing of high-quality prey with prey of inferior quality may be beneficial as long as toxic prey is not included; mixed diets including toxic prey may also be toxic even if higher-quality prey is included.

Toft (unpubl. data) tested these generalizations in a comparable experiment with *Paradosa prativaga* and prey mainly from European agricultural fields. This study revealed no positive effects of dietary mixing, but confirmed the low quality of mixed diets consisting of toxic and higher-quality prey. Thus, the most consistent outcome in these experiments was not a positive mixing effect, but that of toxic prey eliminating the possible benefits of higher-quality prey.

These results clearly show that under the experimental conditions, the spiders were unable to select the most profitable diet from the mixture of good and bad prey available. In some cases (*F. candida* and fruit-flies) acceptance of the toxic prey led to a quick death of the spider in spite of high availability of good prey. So far, there is no information available on the impact of toxic prey on spiders in the field, or on whether spiders in the field are better able to avoid consuming these prey.

ACQUIRED AVERSION AGAINST DETERRENT OR TOXIC PREY

What mechanisms do spiders have to reduce or avoid consumption of poor-quality or toxic prey? Clearly, smell or taste may act as deterrents, perhaps as signals of unpalatability or toxicity. Thus, Bilde & Toft (1994) found reduced acceptance by a carabid beetle of fruit flies coated with homogenate of an aphid or fungus gnat. The response is rarely all-or-none, however. Prey species may be classified according to the spiders' response to them: (a) Some potential prey types are never even attacked by spiders; spiders may have an inherent selectivity against them (*cf.* Nentwig 1987). (b) Other prey types are attacked but discarded uneaten. The difference between this group and the first may be only the strength of the signal that informs the spider about the unpalatability of the prey: if perceived at a distance attack is prevented. (c) Many prey types are accepted readily and eaten on several encounters, but eventually rejected: an acquired aversion has developed. These prey must be moderately deterrent at most. (d) Prey that do not induce aversions: palatable prey. Most often these are high- or intermediate quality prey. (e) Prey that do not induce aversions but are nevertheless toxic (*e.g.*, *F. candida*). These prey may be non-deterrent (*i.e.*, palatable) and spiders (at least young individuals) may die even if the prey are only part of a mixed diet. Tolerance may eventually be induced (see below).

Acquired prey aversions occur when the spider's preference for a prey is reduced following consumption of similar prey, and are probably the main mechanism for limiting consumption of potentially toxic food (Bernays 1993). Several questions arise concerning their specificity and duration. Is an aversion associated with a certain taste of the prey,

with its morphology/behavior or with both? Do spiders learn to associate smell/taste and other prey characteristics in order to be able to avoid poor prey? General answers cannot be given at the moment, but two examples indicate that both taste and behavior can be important for prey recognition. Toft (1997) studied intra- and interspecific aversions of *P. prativaga* against three species of cereal aphids that are similar in behavior and perhaps also in chemical detergency. Induction of aversion was graded in terms of the number of aphids needed to create it, reflecting a difference in palatability of the aphids to the spider. Also, the duration of the aversion (*i.e.*, the time until the next aphid was accepted) depended on which aphid induced the aversion. However, no matter which aphid induced the aversion, the "aversive" spider showed no differential response in encounters with new aphids. Thus, the motivation to attack was determined by the aversion rather than by the aphid actually confronting the spider, *i.e.*, irrespective of its palatability.

In another experiment with *Schizocosa* sp., the spiders' responses to low-quality fungus gnats were recorded (Toft & Wise 1999b). Spiders were offered prey sequentially and allowed to eat them one at a time. The next prey was offered when the spider had eaten the previous one completely or repeatedly rejected it. In one series only fungus gnats were offered; in a second series only fruit-flies; in a third series fungus gnats and fruit flies were offered alternately. Both prey types were accepted initially, and fruit flies continued to be accepted and eaten completely until satiation in both series. Fungus gnats, however, were often rejected after 4–6 had been consumed, with no difference between the single-prey and two-prey series. In the series given only fungus gnats, most spiders eventually ignored the fungus gnats completely. Presumably, they relied on their experience from the last several captures that only fungus gnats were available and used behavior (flying insect) as the cue to prey recognition. In the mixed treatment, where there was a 50% chance that a flying insect would be a palatable one, the spiders continued to catch fungus gnats, only to release them (mostly alive) when they recognized their identity by taste.

Aversions may modify active prey choice at any of the successive stages of the capture

process (cf. Endler 1991). Following recognition of a potential prey, the spider may completely ignore it, or attack-and-retreat if the prey's unpalatability is recognized during attack (but before or at the bite). In the subjugation phase (following bite or wrapping) the prey may be left dead or released alive. In the consumption phase, partial consumption may signify an aversion. Notice that acceptance/rejection is not all-or-none but a graded response, which reflects its conditional nature. Spiders should become more selective when prey availability is high (Riechert 1981; Riechert & Luczak 1982; but see Riechert 1991), or selectivity may depend on an acquired aversion which may develop gradually. As argued by Riechert & Luczak (1982) rejection should occur as early as possible in the predatory sequence. However, acquired aversions indicate that knowledge about the prey depends on experience which takes time to gain, and the information obtained may be uncertain. In the fungus gnat experiment described above (Toft & Wise 1999b), the spiders at first accepted and ate the prey. However, as experience accumulated, they stopped eating (discarded partly eaten prey; released captured prey, very often alive), and eventually stopped attacking the prey (retreating, ignoring the prey). Whether refusing to eat subsequently leads to ignoring of the prey probably depends on the certainty with which the spider is able to identify the prey at a distance. The example indicates that this ability depends not only on the spiders' "knowledge" of (experience with) the prey characteristics, but also on the spider's experiences (expectations) with respect to what prey is available.

An aversion reduces the amount of a poor-quality prey that a spider consumes. However, some poor-quality prey may contribute positively in mixed diets. Thus, complete exclusion from the diet is only advantageous if the prey is always detrimental. A limited duration of an aversion may thus serve to secure a constantly low intake rate, which balances nutrient benefits and toxic damage to the positive side, thus creating a synergistic effect. Toft (1997) measured the duration of aphid aversions in a wolf spider to be mostly < 24 hours. Since only about two aphids were needed to create the aversion in the first place, and probably fewer are needed to reestablish

one, the daily rate of feeding on aphids will be kept quite low. In quantitative estimates with *P. prativaga*, consumption of aphids were only $\frac{1}{10}$ or less of the spider's food demand as determined with fruit flies (Toft 1995).

For some prey types, however, aversions do not protect the spider against toxic overload. Duration of the aversion against the collembolan *F. candida* (animals from USA) was of the same order of magnitude as for aphids, up to ca. 24 hours. This was too short to prevent chronic inhibition of feeding and growth in *Schizocosa* (Toft & Wise 1999b). In similar tests with *P. prativaga* and (presumably) the same collembolan species from Europe, an aversion could not be induced (D. Mayntz unpubl. data). With constant availability this Collembola is lethal to *P. prativaga*. However, surviving hatchlings raised on fruit flies with a limited supplementation of *F. candida* eventually developed a partial resistance to *F. candida*. After 5–6 weeks of inhibited growth the young spiders showed compensatory growth and caught up with the fruit fly controls in a few weeks' time (Toft unpubl. data). Such induced resistance to toxic prey may explain why large juvenile *Schizocosa* were not inhibited by *F. candida*, even though small juveniles were (Toft & Wise 1999b). Nentwig (1985) described digestive modifications in a spider following prolonged feeding on KCN-treated prey.

Turnbull (1960) and Riechert & Luczak (1982) noted neophobia, i.e., reluctance to accept unfamiliar prey that were later readily accepted, in two web-spinning spiders. We have not observed this in wolf spiders, but it may be more prevalent in web-spinners in which the web may intercept large and dangerous prey.

NUTRITIONAL QUALITY OF PREY

Greenstone's (1979) work on prey selection in *Pardosa ramulosa*, indicating nutritional self-selection (cf. Waldbauer & Friedman 1991) for essential amino acids, is still unique. The huge divergence in food quality of potential prey species demonstrated above should leave us more open to accept this possibility. If prey are deterrent or toxic, this fact may completely override any differences in nutritional composition. However, the improved hatching success of *Erigone atra* eggs from females given a mixed fruit fly-aphid diet in-

icates that even low consumption of the poor-quality aphid gave a significant nutrient supplement to the fruit flies (Toft 1995). Also, palatable prey may differ in nutrient quality. Several authors have stated that fruit flies are nutritionally insufficient for complete development of spiders (Miyashita 1968; Riechert & Harp 1987). Recent studies show that nutrient additions to the standard fruit fly medium create flies of enhanced quality to spiders (Kristensen & Toft unpubl. data; Mayntz & Toft unpubl. data). Wolf spider hatchlings fed flies raised on standard and nutrient-improved media, respectively, show differences in survival and growth rates after six weeks. Thus, spiders may enhance their fitness by selecting the most nutritious prey species and even the most nutritious individuals of each species, if that is possible. It can be hypothesized that nutritional selectivity increases with degree of nutritional imbalance, which is most likely to develop when a limited range of prey species is available, as is the case in most feeding experiments. Greenstone's (1979) results were obtained in a situation where diversity of potential prey was limited to three species.

Toft (1996) proposed a graphical model predicting the relationship between a predator's tolerance (i.e., maximal consumption capacity) to various types of prey and its performance if the diet is restricted to one prey type. If prey are deterrent or toxic and consumption capacity is therefore low, the predator is unable to reach satiation on this prey and fitness will be low. If prey is non-toxic and palatable, the predator may reach satiation on this prey type. If it is also of optimal nutrient composition, fitness (growth or reproduction) is maximal on a feeding rate equivalent to the maximal rate at which food can be converted into spider tissue (or eggs). If the prey is deficient in essential nutrients, the spider may to some degree compensate by increasing consumption at the expense of food utilization. Thus, the model predicts an increased consumption rate of nutritionally deficient prey associated with a lowered benefit.

A test of these predictions was provided by Marcussen et al. (in press) in experiments with the linyphiid spider *Erigone atra*. A collembolan (*Folsomia fimetaria*) was clearly toxic. Both consumption and reproduction were low, and supplementing a fruit fly diet

with this collembolan reduced reproduction compared to the pure fruit fly diet. Another collembolan (*Isotoma anglicana*) was found to be of very high quality, significantly better than fruit flies, in terms of both number of egg-sacs and eggs/sac produced by the females. However, quantification of daily consumption rates showed that the spiders consumed $> 1.5\times$ more fruit fly mass than *I. anglicana* mass. Thus, the spiders attained the maximal reproductive rate by a moderate consumption rate of nutritionally high-quality prey. A result that can be interpreted in the same vein is the finding that limited and unlimited rations of fruit flies gave the same reproductive output in *E. atra* (Toft 1995). Presumably the limited feeding rate was nutritionally superior due to more efficient nutrient extraction of each prey item (Toft 1996).

An interesting consequence of these results is that fitness maximization is achieved by optimal balancing of nutrients rather than by maximization of energy consumption.

CONCLUSIONS

This review has demonstrated that two conditions for the evolution of prey selectivity of spiders, viz. the differences in food quality of various prey and the consequences of prey quality for spider fitness, are met. In several experiments, however, poor performance of the spiders proved that what the spiders chose was not the optimal selection from the available prey mixture. Benefits of prey mixing were found, but so far there has been no experimental demonstration that spiders can choose the optimal diet when a mixture of prey of various qualities is available. Also, nutritional self-selection still needs to be experimentally established. Selectivity is evident in the spiders' responses to some (but not all) low- and poor-quality prey types, which are accepted at a rate much below availability. Acquired aversions are probably the main behavioral mechanism for reducing consumption of toxins and are the most prominent expression of selective prey choice. A short aversion memory may serve to balance toxic damage with the nutritional benefit of a diverse diet.

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MECHANISMS UNDERLYING THE EFFECTS OF SPIDERS ON PEST POPULATIONS

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ABSTRACT. Assemblages of spider species can make significant reductions in pest numbers that are of value to the farmer. A group of spider species with complementary niches leaves few refuges for the pest in space or time. Spiders usually exert an influence on pest numbers in concert with other natural enemies, and spiders are sometimes the dominant component. In addition to killing pests by direct attack, spiders cause pest mortality by dislodging them from plants or trapping them in webs. If the pest is distasteful, or if it is the dominant prey type available, spiders may kill more than they consume, which increases the rate of pest kill per unit of spider food demand. The implications for pest control, of various types of interaction between spiders and other natural enemies, are explored in this paper. Interactions with specialist natural enemies usually result in complementary effects, enhancing pest control. Specialists reduce the density of pests to levels where spiders can prevent resurgence. Specialists foraging on the crop may flush pests off the plant to be killed by ground-zone spiders. Although hyperpredation (i.e., predators killing other predators) may disrupt biological control occasionally, it is considered that the wide range of competitive interactions between natural enemies, in general, promotes diversity and stability of the natural enemy community and generates a robust basis for pest control.

There are currently in excess of 3000 described genera of spiders (Coddington *in lit.*), more than 50,000 species are predicted to be living on the planet, and they are the dominant insectivores in some terrestrial ecosystems (Thompson 1984). They are of economic value to man because of their ability to suppress pest abundance in agroecosystems. Faced with the need to reduce pesticide usage on the world's crops and optimize natural biological control, full investigation of the means by which spiders influence pest abundance is long overdue. Also, in recent years, there has been a realization by ecologists that components of agroecosystems are tractable to manipulate and that spiders are convenient model organisms. Consequently, there are a growing number of investigations in which spiders in agroecosystems are used as tools to gain fundamental insights into the role of generalist predators in community and ecosystem function.

This review is a brief exploration of the major routes by which spiders can influence the abundance of invertebrate pests.

DIRECT PREDATION BY SPIDERS

By spider assemblages.—Individual species of spider may, occasionally, make suffi-

cient impact on a herbivore population for measurable effects on plant production to be registered (Louda 1982), but there is currently no evidence for this in agriculture. Consideration of some aspects of the biology of spiders (e.g., generation times and functional and numerical responses) leads to the conclusion that individual spider species are unlikely to regulate pest populations (Riechert & Lockley 1984; Riechert 1992; Wise 1993). However, when assembled into groups of species, as is the norm in agriculture (Sunderland et al. 1997), they often contribute to significant reductions in pest numbers that are of value to the farmer. In an individual-based model, increasing the number of spider species contributed significantly to prey limitation (Provencher & Riechert 1994). Nentwig (1982) found indications that the size-frequency structure of the arachnofauna matches that of their potential prey, and he suggested a significant role for spiders as a multi-predator complex for reducing a multi-prey complex. Experimental field manipulations, of the mean abundance of spider assemblages, has demonstrated a significant level of impact of spiders on leafhoppers in rice (Orazé & Grigarick 1989), on caterpillars in taro (Nakasuji et al. 1973), cotton (Mansour 1987) and orchards

(Mansour et al. 1980), scale insects in orchards (Mansour & Whitcomb 1986), and various pests in vegetables (Riechert & Bishop 1990) and old fields (Provencher & Riechert 1994; Riechert & Lawrence 1997). The effect of spider predation on pest populations can be sufficient to reduce significantly levels of crop damage (Riechert & Bishop 1990; Carter & Rypstra 1995). Spider species often have complementary niches (Whitcomb 1974; Nyffeler & Sterling 1994), segregating in terms of dimensions such as vertical location, diel cycle and foraging mode (Marc & Canard 1997), and, as an assemblage, may be able to kill all growth stages of a pest, including the eggs (Nyffeler et al. 1990). This means that there are fewer refuges for the pest in time or space (less "enemy-free space"—Jeffries & Lawton 1984), and this is to the benefit of pest control (Murdoch 1990).

By a group of natural enemies including spiders.—Spiders need not act alone to be of value in agriculture. They also have a valid role as one component of a larger complex of natural enemies with the potential to keep pests at non-damaging levels. They play this role in the control of Colorado potato beetle (Cappaert et al. 1991) and mosquitoes (Service 1973), for caterpillar control on cotton (Gravena & Da-Cuhna 1991) corn (Coll & Bottrell 1992; Clark et al. 1994) and in forestry (Mason et al. 1983), against aphids on cotton (Chen et al. 1994) and apple (Wyss et al. 1995), and against hoppers and other pests on rice (Sawada et al. 1993; Kamal & Dyck 1994; Settle et al. 1996). As would be expected, the relative contribution of spiders compared to other natural enemies varies with crop and season and in response to many other factors. Spiders were not the dominant element in the predatory complex controlling *Helicoverpa* spp. caterpillars on cotton in Australia (Bishop & Blood 1981). However, on cotton in Texas more than 80% of predators observed to kill cotton fleahopper (*Pseudatomoscelis seriatus*) were spiders (Nyffeler et al. 1992); and they accounted for 73% of the net value of predators, compared to 27% for insects (Sterling et al. 1992). Spiders are the most abundant natural enemies in cotton fields throughout China (55–81% of all natural enemies); and they play a key role, together with the other dominant natural enemies, in suppressing pest populations (Zhang 1992).

ADDITIONAL ATTRIBUTES OF VALUE FOR PEST CONTROL

Pest dislodgement.—The foraging behavior of spiders on crop vegetation may disturb pest aggregations and may also cause the disturbed pests to walk or fall off the plants. This can reduce the pest population if the physical conditions on the ground cause rapid mortality (e.g., aphid survival times of only a few minutes at ground temperatures above 40 °C in North American field crops; Dill et al. 1990), or if they cannot easily regain the plants, or if they move into danger zones with greater probabilities of attack by natural enemies. It is possible that pest species belonging to many Orders are dislodged by spiders, but the literature emphasizes an effect on Lepidoptera. In manipulative experiments in apple orchards (Mansour et al. 1981) and in taro fields (Nakasugi et al. 1973; Yamanaka et al. 1973) approximately one third of caterpillars were dislodged, and the authors considered that the majority of dislodged individuals would be unable to regain the plant. In these examples dislodgement resulted in death of the pest. Under less extreme conditions the loss of feeding time resulting from dislodgement may be expected to reduce plant damage and also to reduce the rate of increase of the pest population.

Death of pests in webs not caused by spider predation.—Small pests, such as thrips, midges and aphids, may die by being caught in the webs of large spiders, even when they are ignored by the spider (Nentwig 1987). Alderweireldt (1994) identified 319 prey items in webs of linyphiid spiders in maize fields in Belgium. Spiders were feeding on only 184 of these prey items. Linyphiidae, Dictynidae, Theridiidae and Agelenidae do not renew their webs daily, and feed infrequently (Nyffeler et al. 1994a), so these families may contribute to pest control by the action of their webs. First instars of the cereal aphid *Sitobion avenae* did not escape from webs of non-attacking satiated adult female linyphiid spiders, *Lepthyphantes tenuis* (Sunderland et al. 1986). The proportion of *S. avenae* falling into webs (or sticky traps to simulate webs) that are first instars is typically 10–20% (Fraser 1982; Kennedy 1990). The mean duration of web-site tenacity in this species is less than two days (Samu et al. 1996), so the number of webs

may exceed the number of web-makers. In this study (Samu et al. 1996) nearly all *L. tenuis* webs contained uneaten *S. avenae* and none of the 60 observed spiders were feeding. Thus the potential of webs to kill pests, in the absence of spider attack, can be a relevant consideration for biological control.

Wasteful killing, partial consumption and the wounding of pests.—Under certain circumstances the predator may kill a pest but subsequently ingest little (partial consumption) or none (variously referred to in the literature as “superfluous killing” and “wasteful killing”) of the pest’s biomass. This is advantageous for pest control because it will result in more pests being killed per unit of spider food demand. These behaviors are usually observed when prey are plentiful (or when a small spider is able to overcome a large prey) and the spider is nearly or completely satiated. The seemingly inappropriate behavioral overshoot of continuing to kill when enough food to induce satiation has already been secured may be due to the time lag between prey capture and ingestion associated with the spider’s extra-oral digestion system (Riechert & Lockley 1984). This is the arachnid equivalent of the gut compartmentalization theory proposed for insects (Johnson et al. 1975). There are examples of wasteful killing at high prey density for Clubionidae and Linyphiidae against aphids (Provencher & Coderre 1987; Mansour & Heimbach 1993), for Linyphiidae (DeKeer & Maelfait 1988) and Lycosidae (Samu & Biro 1993) against flies, and for Araneidae against hymenopteran parasitoids (Smith & Wellington 1983). Partial consumption has been recorded for Thomisidae and Lycosidae at high densities of *Drosophila* prey (Haynes & Sisojevic 1966; Samu 1993). These examples all refer to laboratory studies and it is not known how prevalent wasteful killing and partial consumption are under field conditions. Predators are not 100% efficient, and it is known that wounded prey may die following unsuccessful attacks by coleopteran (Doane et al. 1985) and dipteran (Griffiths et al. 1984) predators. It is likely that spiders, also, cause some pest mortality by wounding leading to fatal infection or loss of haemolymph, but this will be difficult to quantify in the field.

Mansour & Heimbach (1993) recorded a high rate of wasteful killing of the cereal

aphid *Rhopalosiphum padi* by spiders, even at low aphid density. *R. padi*, in common with other species of cereal aphid, is a poor quality food for spiders (Toft 1995). They may find it distasteful and can develop an aversion to it, but such aversions persist for only a few hours (Toft 1997). Prey that cause an aversion response by the spider may be ignored, or attacked and released intact, or released wounded or dead, or killed and partially consumed (Nentwig 1985), depending on many variables, including spider hunger and degree of naivete (Toft 1997). Such behavior would not be expected from a specialist natural enemy. When food availability is dominated by a non-preferred pest species (e.g. aphids constituting 83% of prey items in webs of *L. tenuis* in maize; Alderweireldt 1994) the spider population might even kill more pests than if the pests were a high-quality preferred food, because spiders would remain unsatiated. This prey sampling-aversion-wasteful killing syndrome also raises questions about our methodologies for determining the kill rate of spiders on pests, especially for species that do not construct webs. Post-mortem methods, such as electrophoresis, radio-tracers and antibody techniques (Sunderland 1988; Greenstone 1996), would fail because no ingestion has taken place. Quantitative methods based on direct observation of food being eaten by spiders in the field (e.g., Edgar 1970) would underestimate the impact on pests, because the probability of observing a kill and rejection incident is much lower than that of a kill and consume incident (the former being of shorter duration than the latter).

SPIDERS IN COMMUNITIES

Spiders in agroecosystems are components of species-rich communities of herbivores, detritivores and natural enemies. The effect of a spider species on a pest population may be enhanced if the spider population increases rapidly in response to a rich supply of nutritious alternative prey (Jeffries & Lawton 1984; Axelsen et al. 1997). However, if the pest species is less-preferred than the alternative prey, the net effect of these opposing processes on the level of pest control will be difficult to predict (Bilde & Toft 1994). Selective predation by spiders in relation to the size of pest taken (Nentwig & Wissel 1986) can alter the mean body size of the pest pop-

ulation, modifying its vulnerability to other size-dependent natural enemies in the community (Strauss 1991). Some additional examples of interactions between spiders and other natural enemies, with implications for pest control, are described below.

Predation of moribund pests.—Predation by spiders of moribund parasitized pests (i.e., living pests that will be killed eventually by the developing parasitoid) is counter-productive to biological control because the mortality of these pest individuals is already assured, and spider predation will reduce the size of the next generation of parasitoids. Predation of moribund parasitized pests could, however, be of value to the farmer in cases where the moribund pest continues to damage the plant significantly, or reproduces before death (Sunderland 1996). Moribund pests often have phenologies, distributions, activity, defenses and palatability that are different from the healthy pest (Sunderland 1996), but there is very little information in the literature concerning how this influences the probability of capture by spiders (Coll & Bottrell 1992). Predation of moribund diseased pests could be beneficial if the spider spreads the disease to other individuals in the pest population. For example, it is considered likely that *Oxyopes salticus* is an important disseminator of *Anticarsia gemmatilis* Nuclear Polyhedrosis Virus in USA soybean (Kring et al. 1988). It is regrettable that interactions between predators and moribund pests are rarely taken into account in comparisons of the relative effectiveness of predators, parasitoids and pathogens in biocontrol (Hawkins et al. 1997).

Interactions between spiders and specialist predators.—*Pest density:* Spiders, as generalist predators, can be present in a crop, feeding on alternative prey, before the pest arrives. High spider-pest ratios early in the season (e.g., Wheeler 1973; Zhang 1992) may reduce the pest increase rate sufficiently to enable later-arriving specialist natural enemies to suppress the pest population below the economic threshold, a conclusion also reached from metabolic pool modeling exercises (Axelsen et al. 1997). This is a finely-balanced relationship that can also have a negative outcome if synchronization is inadequate. For example, if generalists depress pest density below the oviposition threshold of immigrant specialists (Honek 1980; Ghanim et al 1984),

the specialists are likely to leave the field in search of higher pest densities elsewhere, and the generalists may then be unable to prevent a pest outbreak occurring. Generalists and specialists do, however, work together harmoniously, if not synergistically, in many agroecosystems (e.g., Zhang 1992). In perennial systems, this is sometimes because specialists reduce pest density, in one year, to a level from which generalists are able to prevent resurgence in later years (Mason & Torgersen 1987; Roland & Embree 1995). Specialist predators, by themselves, tend to be unreliable (except for crops with economics that permit rear-and-release strategies) because their densities are highly variable from year to year (Aebischer 1991). In contrast, it has been suggested (Sunderland et al. 1996) that the densities of generalists (e.g., spider assemblages) are buffered, in that a deficiency in the numbers of any one species in a given year is very likely to be counterbalanced by a superabundance of another species within the same guild.

Spatial effects: Pests, such as aphids and caterpillars, are dislodged by foraging parasitoids and predators, and especially by specialists such as aphidophagous coccinellids (see review in Sunderland et al. 1997). Spider assemblages are often vertically stratified in crops (e.g., Provencher et al. 1988; Marc & Canard 1997), and many spider species are confined to the ground zone or lower strata of vegetation (Wheeler 1973; Leathwick & Winterbourn 1984; Heong et al. 1990). In U.K. winter wheat, the proportion of fallen aphids that climb back onto plants is negatively related to the density of ground predators (Winder 1990; Duffield et al. 1996). Sixty-one out of 109 species of spider in this crop are confined to the ground zone (Sunderland et al. 1988), and the webs of linyphiids can cover 50% of the ground surface below the crop (Sunderland et al. 1986). Thus it is clear that spiders, and other ground predators, will make a greater contribution to aphid control in this crop in situations where aphids are flushed off the crop by specialist natural enemies.

Competitive interactions between predators.—Cannibalism, intra-specific competition and territoriality (Wise 1993) may result in self-limitation of the density of a given spider species, and inter-specific interactions, including interference competition (Spiller

1984; Moran & Hurd 1994), can result in further reductions in density. Complete elimination of a competing species from the crop may be averted if the intensity of competition is ameliorated by the action of a top predator reducing the density of the dominant competitor (i.e., exploiter-mediated coexistence, as applied to predators). An example of a top predator that might fulfil this role, in USA cotton, is the green lynx spider (*Peucetia viridans*), which is strongly araneophagous (Nyffeler et al. 1987). Interactions such as these promote spider biodiversity and, in addition, cannibalism and hyperpredation (i.e., predators killing predators) may buffer the spider community (i.e., prevent localized species extinctions) during short-term dearth of herbivore and detritivore prey. These mechanisms reduce the availability of enemy-free space to pests, and their effects are enhanced by a behavioral flexibility on the part of predators that permits them to make short-term niche shifts (Jeffries & Lawton 1984; Polis et al. 1989). For example, hunting spiders in USA field crops are highly polyphagous, but can narrow their feeding niche significantly when a suitable prey species reaches high numbers (Nyffeler et al. 1994b).

Some species of spider have been shown to make little impact on other predators (Nentwig 1975; Lockley & Young 1987; Jmhasly & Nentwig 1995), but others are significant predators of spiders, ants, lacewings, ladybirds, and predatory Heteroptera (Nentwig 1986; Nyffeler et al. 1987; Sengonca & Klein 1988; Heong et al. 1992; Nyffeler et al. 1994b; Dinter 1998). Hyperpredation is valuable in promoting diversity and stability of the natural enemy community, but is occasionally detrimental to pest control when intense predation of one predator by another releases a pest from a former level of satisfactory biological control (Rosenheim et al. 1995). Spiders are included in the natural enemy complex implicated as reducing the effectiveness of lacewing release for leafhopper control in vineyards (Daane et al. 1996) and of pentatomid release for suppression of Colorado potato beetle (Hough-Goldstein et al. 1996).

CONCLUSIONS

There are indications from the literature of many mechanisms whereby spiders can affect the abundance of invertebrate pests. Direct

predation, pest dislodgement and wasteful killing (by both spider and web) reduce pest abundance, whilst predation of moribund pests and IGP may destabilize existing natural control and trigger indirectly an increase in the pest population. The relative importance of these various pathways in any given agroecosystem, and whether major pathways differ between agroecosystems, is not known. Answering these questions is consistent with the development of a "community approach" to biological pest control and spiders are especially apt subjects of study in this context because they are known to exert their influence on pest populations as species assemblages and in concert with other groups of natural enemies.

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PREY SELECTION OF SPIDERS IN THE FIELD

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ABSTRACT. In this article, an overview of the general feeding patterns of common agroecosystem spiders is presented. Five groups of web-weavers (Tetragnathidae, Araneidae, Theridiidae, Linyphiidae, Dictynidae) and five groups of hunters (small-sized Oxyopidae, large-sized Oxyopidae, Thomisidae, Salticidae, Lycosidae) are analyzed comparatively (based on 40 prey analyses previously published by various European and US authors). Fewer than 10 insect orders, as well as the order Araneae, make up the bulk of the prey of these spiders. Web-weavers and hunters both basically feed on the same prey orders, but in different proportions. The observed differences reflect in part the very diverse range of life styles and foraging modes exhibited by the various spider groups and, to some extent, differences in prey availability. Web-weavers are almost strictly insectivorous (insects constituting > 99% of total prey). Hunters, however, exhibit a mixed strategy of insectivorous and araneophagic foraging patterns (insects constituting ≈ 75 –90% of total prey). Diet breadth computed with the Inverted Simpson Index was, on average, significantly higher in the hunting spiders than the web spiders. There seems to be a consistent trend of greater diet breadth of the hunters compared to the web-weavers in agroecosystems. Overall, spider individuals of small size (including large percentages of immatures) numerically dominate the faunas of field crops, and these feed primarily on tiny prey (< 4 mm in length).

Information on how prey selection in the field operates is a prerequisite to a quantitative assessment of the spiders' potential as biological control agents in agroecosystems. Prey selection has been defined by Hassell (1978) as follows: "Preference for a particular prey is normally measured in terms of the deviation of the proportion of that prey attacked from the proportion available in the environment." Most authors who studied the prey of spiders failed to record the availability of potential prey in the environment probably due to technical difficulties. Thus, corresponding data on the actual and potential prey are scarce; and, consequently, only a limited number of prey selection studies on spiders following Hassell's approach exist (e.g., Uetz et al. 1978).

Another approach to searching for patterns of prey selection is to analyze a large set of data on the actual prey of different spider groups (with very differing life styles and foraging modes) and to compare the degree to which utilization of the various prey taxa differs. Numerous published field studies on the actual prey of spiders are available for such an investigation (see reviews by Nyffeler 1982; Nentwig 1987; Riechert & Harp 1987; Wise 1993; Nyffeler et al. 1994a, b). In the current investigation, five groups of web-

weavers (Tetragnathidae, Araneidae, Theridiidae, Linyphiidae, Dictynidae) and five groups of hunters (small-sized Oxyopidae [i.e., *Oxyopes salticus*], large-sized Oxyopidae [i.e., *Peucetia viridans*], Thomisidae, Salticidae, Lycosidae), representing nine families, are analyzed comparatively. These selected groups are among the most common spider predators in agroecosystems (Nyffeler et al. 1994b) and, thus, are of particular interest from the point of view of biological control. Descriptions of the life styles and foraging modes of these 10 spider groups are given by Rypstra (1982), Nentwig (1987), Wise (1993), and Nyffeler et al. (1994a, b).

METHODS

For each of the 10 spider groups the relative taxonomic composition of the diets (mean \pm SE of 4 different prey analyses) was assessed (Tables 2, 3). Overall, 40 different prey analyses (based on observational data from 31 published studies [see Table 1]) have been processed. To determine relative feeding specialization, the diet breadth B (= diversity of arthropod orders in the diet) was computed for each spider group by means of the Inverted Simpson Index (see Levins 1968; Colwell & Futuyma 1971) (Table 4). Diet breadth is inversely related to ecological specialization

Table 1.—Field studies used for the assessment of the relative taxonomic composition of the diets of ten spider groups. Habitats: SO = soybean, CO = cotton, PE = peanuts, AA = alfalfa, WW = winter wheat, OA = oats, MA = maize, MM = mown meadow, VE = vegetables, NC = noncrop.

Spider group	Habitat	Area	Author(s)
Tetragnathidae			
<i>Tetragnatha laboriosa</i>	SO	USA	LeSar & Unzicker (1978)
<i>Tetragnatha laboriosa</i>	SO	USA	Culin & Yeargan (1982)
<i>Tetragnatha laboriosa</i>	CO	USA	Nyffeler et al. (1989)
<i>Tetragnatha extensa</i>	WW	Europe	Nyffeler & Benz (1979)
Araneidae			
<i>Acanthepeira stellata</i>	CO	USA	Nyffeler et al. (1989)
<i>Argiope aurantia</i>	CO	USA	Nyffeler et al. (1987a)
<i>Neoscona arabesca</i>	CO	USA	Nyffeler et al. (1989)
<i>Neoscona arabesca</i>	SO	USA	Culin & Yeargan (1982)
Theridiidae			
<i>Latrodectus mactans</i>	CO	USA	Nyffeler et al. (1988a)
<i>Achaearanea riparia</i>	WW	Europe	Nyffeler & Benz (1988a)
<i>Theridion impressum</i>	WW	Europe	Nyffeler (1982)
<i>Theridion impressum</i>	OA	Europe	Nyffeler & Benz (1979)
Linyphiidae			
various Erigoninae	MA	Europe	Alderweireldt (1994)
various Erigoninae	WW	Europe	Sunderland et al. (1986)
various Erigoninae	WW	Europe	Nyffeler & Benz (1988b)
various Erigoninae	MM	Europe	Nyffeler (1982)
Dictynidae			
<i>Dictyna segregata</i>	CO	USA	Nyffeler et al. (1988b)
<i>Dictyna arundinacea</i>	WW	Europe	Heidger & Nentwig (1989)
<i>Dictyna arundinacea</i>	NC	Europe	Heidger & Nentwig (1986)
<i>Dictyna montana</i>	NC	Africa	Nentwig (1987)
Oxyopidae (small-sized)			
<i>Oxyopes salticus</i>	CO	USA	Nyffeler et al. (1987b)
<i>Oxyopes salticus</i>	CO	USA	Nyffeler et al. (1992a)
<i>Oxyopes salticus</i>	CO	USA	Lockley & Young (1987)
<i>Oxyopes salticus</i>	PE	USA	Agnew & Smith (1989)
Oxyopidae (large-sized)			
<i>Peucetia viridans</i>	CO	USA	Nyffeler et al. (1987c)
<i>Peucetia viridans</i>	CO	USA	Nyffeler et al. (1992a)
<i>Peucetia viridans</i>	NC	USA	Turner (1979)
<i>Peucetia viridans</i>	NC	USA	Randall (1982)
Thomisidae			
<i>Misumenops</i> spp.	PE	USA	Agnew & Smith (1989)
<i>Misumenops</i> spp.	CO, NC	USA	Dean et al. (1987)
<i>Xysticus emertoni</i>	NC	USA	Morse (1983)
<i>Xysticus</i> spp.	MM	Europe	Nyffeler & Breene (1990a)
Salticidae			
<i>Phidippus audax</i>	CO, NC	USA	Dean et al. (1987)
<i>Phidippus audax</i>	CO, NC	USA	Young (1989)
<i>Phidippus audax</i>	VE	USA	Riechert & Bishop (1990)
<i>Phidippus johnsoni</i>	NC	USA	Jackson (1977)
Lycosidae			
<i>Pardosa ramulosa</i>	AA	USA	Yeargan (1975)
<i>Pardosa</i> spp.	PE	USA	Agnew & Smith (1989)
<i>Pardosa</i> spp.	WW	Europe	Nyffeler & Benz (1988c)
<i>Pardosa amentata</i>	NC	Europe	Hallander (1970)

Table 2.—Relative taxonomic composition of the diets of various web-weavers [for each spider group a mean ± SE, based on 4 different prey analyses has been computed]. ¹ LeSar & Unzicker (1978); Nyffeler & Benz (1979); Culin & Yeargan (1982); Nyffeler et al. (1989). ² Culin & Yeargan (1982); Nyffeler et al. (1987a); Nyffeler et al. (1989) [data for 2 species]. ³ Nyffeler (1982); Nyffeler & Benz (1979, 1988a); Nyffeler et al. (1988a). ⁴ Nyffeler (1982); Sunderland et al. (1986); Nyffeler & Benz (1988b); Alderweireldt (1994). ⁵ Nentwig (1987); Nyffeler et al. (1988b); Heidger & Nentwig (1986, 1989).

Diet item (in %)	Tetragna- thidae ¹ (<i>Tetragnatha</i>)	Araneidae ² (<i>Acan- thepeira</i> , <i>Argiope</i> , <i>Neoscona</i>)	Theridiidae ³ (<i>Latrodectus</i> , <i>Achaearanea</i> , <i>Theridion</i>)	Linyphiidae ⁴ (<i>Erigoninae</i>)	Dictynidae ⁵ (<i>Dictyna</i>)	Overall mean
Homoptera	51 ± 16	36 ± 7	26 ± 9	33 ± 8	21 ± 13	33 ± 5
Diptera	40 ± 17	21 ± 6	15 ± 7	9 ± 2	64 ± 15	30 ± 6
Hymenoptera	3 ± 1	7 ± 2	32 ± 17	2 ± 1	7 ± 3	10 ± 4
Collembola	0 ± 0	0 ± 0	0 ± 0	48 ± 8	0 ± 0	10 ± 5
Coleoptera	1 ± 1	24 ± 9	13 ± 4	<1 ± 0.2	1 ± 1	8 ± 3
Heteroptera	5 ± 4	3 ± 1	1 ± 1	1 ± 0.5	<1 ± 0	2 ± 1
Lepidoptera	<1 ± 0.7	3 ± 1	1 ± 1	0 ± 0	0 ± 0	<1 ± 0.4
Araneae	0 ± 0	<1 ± 0.2	<1 ± 0.5	<1 ± 0.2	<1 ± 0.2	<1 ± 0.1
Others	0 ± 0	5 ± 4	11 ± 4	6 ± 2	7 ± 2	6 ± 2
Total	100 ± 0	100 ± 0	100 ± 0	100 ± 0	100 ± 0	100 ± 0

(Colwell & Futuyma 1971; Turner 1979). Thus, high *B*-values are characteristic for exceedingly polyphagous predators, whereas low values indicate a more specialised feeding behavior. [Here a specialist feeder is defined as one that exhibits narrow diet breadth in a particular environment.]

RESULTS AND DISCUSSION

Overall, fewer than 10 arthropod orders (Diptera, Homoptera, Hymenoptera, Heterop-

tera, Collembola, Coleoptera, Lepidoptera, and Araneae) make up the bulk of the prey of common agroecosystem spiders all of which are polyphagous predators (generalists) (Tables 2, 3). Dietary mixing seems to be advantageous by optimizing a balanced nutrient composition needed for survival and reproduction (Greenstone 1979; Uetz et al. 1992; Toft 1995). The various spider groups feed basically on the same orders, but in different proportions. The observed differences reflect,

Table 3.—Relative taxonomic composition of the diets of various hunters [for each spider group a mean ± SE, based on 4 different prey analyses has been computed]. ¹ Lockley & Young (1987); Agnew & Smith (1989); Nyffeler et al. (1987b; 1992a). ² Turner (1979); Randall (1982); Nyffeler et al. (1987c, 1992a). ³ Morse (1983); Dean et al. (1987); Agnew & Smith (1989); Nyffeler & Breene (1990a). ⁴ Jackson (1977); Dean et al. (1987); Young (1989); Riechert & Bishop (1990). ⁵ Hallander (1970); Yeargan (1975); Nyffeler & Benz (1988c); Agnew & Smith (1989).

Diet item (in %)	Oxyopidae ¹ (<i>Oxyopes</i>)	Oxyopidae ² (<i>Peuceitia</i>)	Thomisidae ³ (<i>Misumenops</i> , <i>Xysticus</i>)	Salticidae ⁴ (<i>Phidippus</i>)	Lycosidae ⁵ (<i>Pardosa</i>)	Overall mean
Heteroptera	30 ± 10	18 ± 4	18 ± 11	21 ± 11	16 ± 13	21 ± 4
Diptera	14 ± 3	13 ± 5	28 ± 8	17 ± 6	21 ± 7	19 ± 3
Araneae	11 ± 4	13 ± 6	9 ± 3	16 ± 6	24 ± 9	15 ± 3
Hymenoptera	11 ± 5	35 ± 20	16 ± 6	5 ± 5	3 ± 1	14 ± 3
Homoptera	18 ± 4	1 ± 0.5	2 ± 1	14 ± 3	17 ± 5	10 ± 2
Lepidoptera	8 ± 6	9 ± 2	16 ± 7	10 ± 4	3 ± 2	9 ± 2
Coleoptera	<1 ± 0.3	6 ± 1	6 ± 2	13 ± 7	3 ± 2	6 ± 2
Collembola	0 ± 0	0 ± 0	<1 ± 0.2	0 ± 0	8 ± 6	2 ± 1
Others	7 ± 1	5 ± 2	5 ± 2	4 ± 2	5 ± 2	5 ± 1
Total	100 ± 0	100 ± 0	100 ± 0	100 ± 0	100 ± 0	100 ± 0

in part, the diverse range of life styles and foraging modes exhibited by the various spider groups, and to some extent differences in prey availability (see Riechert & Luczak 1982; Nentwig 1987; Nyffeler et al. 1994b).

Web-weavers are almost strictly insectivorous (insects constituting > 99% of total prey) (Table 2). Aggressive encounters among web-weavers occur quite frequently, but rarely result in predation. In a web, the potential victim gets advanced vibrational warning and can flee or be ready to repulse the attacker. During such encounters between web-weavers the inferior individual is usually chased away by its opponent (see Wise 1993). Under conditions of suitable food supply in the form of insects the web-weavers seem to minimize feeding on "dangerous prey" such as spiders. Hunters, however, exhibit a mixed strategy of insectivorous and araneophagic foraging patterns (insects constituting ≈75–90% of total prey) (Table 3). Field populations of several species of hunters had been found to be in a state of undernourishment (see Nyffeler & Breene 1990b). Thus, araneophagy including cannibalism (as an additional feeding strategy to insectivory) may be crucial in sustaining the hunter populations during periods of food shortage (see Wise 1993). "Eating other spiders appears to be an opportunistic occurrence, a larger or faster individual overpowering another in a chance encounter" (Jackson 1992).

Based on the data presented in Tables 2 and 3, the diet breadth (*B*) for spiders was computed with the Inverted Simpson Index (Table 4). The highest value was approximately five times higher than the minimum (*B* = 1.13 vs. 5.58), which indicates considerable between-species differences in diet breadth. Evidently the hunters exhibit on average a less specialized feeding behavior (overall mean diet breadth = 4.20 ± 0.20) compared to the web-weavers (overall mean = 2.61 ± 0.22) (Table 4), the difference between the two overall means being statistically significant (Mann-Whitney *U* test; $U_s = 52.5$; $df = 20, 20$; $P < 0.002$).

The data in Table 3 are almost exclusively based on US sources (3 out of 20 references from Europe), whereas those in Table 2 are from both European and US sources (10 out of 20 references from Europe). The US studies are generally from more southern and warmer

Table 4.—Diet breadth (*B*) of five groups each of web-weaving spiders and hunting spiders; higher values indicate a less specialized feeding behavior (same data used as in Tables 2, 3).

Spider group	Diet breadth <i>B</i>	
	Mean ± SE	Range
Web-weavers:		
Tetragnathidae	1.87 ± 0.40	1.24–2.96
Araneidae	3.42 ± 0.28	2.86–4.19
Theridiidae	3.20 ± 0.60	1.70–4.52
Linyphiidae	2.55 ± 0.30	1.85–3.20
Dictynidae	2.00 ± 0.42	1.13–3.00
Overall mean	2.61 ± 0.22	
Hunters:		
Oxyopidae (<i>Oxyopes</i>)	4.42 ± 0.58	2.76–5.44
Oxyopidae (<i>Peucetia</i>)	4.34 ± 0.34	3.42–4.86
Salticidae	4.38 ± 0.33	3.45–4.89
Thomisidae	3.95 ± 0.44	3.09–5.17
Lycosidae	3.90 ± 0.69	2.65–5.58
Overall mean	4.20 ± 0.20	

latitudes than the European ones (so far, most studies on the natural diets of hunters in crops available in the literature are from the southern US). Furthermore, the majority of US studies were conducted in structurally complex crops such as cotton and soybean fields, whereas most European studies were from cereal crops with a less complex (i.e., prevalently vertical) vegetation structure. Differences in geographic latitude as well as vegetation structure could influence the prey availabilities. Thus, the question arises whether the result of a greater diet breadth of the hunters observed in this study (Table 4) eventually is due to biases in the data set (the web and hunting spiders being studied in different crops and continents). To rule out this possibility, hunters and web-weavers should be analysed under comparable conditions (i.e., in the same field with identical prey availabilities).

Studies in which both hunters and web-weavers were evaluated in the same fields were published by Nyffeler (1982), Nyffeler & Sterling (1994), and Bardwell & Averill (1997). Based on these studies the diet breadth of web spiders and hunting spiders was assessed comparatively (Table 5). In Nyffeler's (1982) study in winter wheat fields near Zurich, Switzerland, hunters (represented by *Pardosa* spp. wolf spiders) had a greater diet

Table 5.—Diet breadth (*B*) of web-weaving spiders vs. hunting spiders in winter wheat, cotton, and cranberry, based on data from: ¹ Nyffeler (1982); ² Nyffeler & Sterling (1994); ³ Nyffeler et al. (1992a); ⁴ Bardwell & Averill (1997).

Crop	Foraging strategy	Spider species	Diet breadth <i>B</i>
WHEAT:	Web-weavers	<i>Tetragnatha extensa</i> ¹	1.24
		<i>Theridion impressum</i> ¹	2.90
		Erigoninae (pooled data) ¹	3.10
		<i>Achaearanea riparia</i> ¹	3.70
	Hunters	<i>Pardosa</i> spp. (pooled data) ¹	4.48
COTTON:	Web-weavers	<i>Tetragnatha laboriosa</i> ²	1.36
		<i>Latrodectus mactans</i> ²	1.70
		<i>Dictyna segregata</i> ²	2.37
		<i>Neoscona arabesca</i> ²	2.86
		<i>Acanthepeira stellata</i> ²	3.29
	Hunters	<i>Oxyopes salticus</i> ³	4.73
		<i>Oxyopes salticus</i> ²	4.76
CRANBERRY:	Web-weavers	(pooled data) ⁴	3.17
	Hunters	(pooled data) ⁴	4.69

breadth than the web-weavers (represented by orb weavers, sheet web-weavers, and tangle web-weavers) (Table 5). Likewise, in Texas cotton fields, the numerically dominant hunters (*Oxyopes salticus* and *Peucetia viridans*) exhibited greater diet breadth than several species of web-weavers (Table 5) (see Nyffeler et al. 1992a; Nyffeler & Sterling 1994). Furthermore, the data presented by Bardwell & Averill (1997) from cranberry bogs in Massachusetts suggest that the hunting spiders exhibited greater diet breadth than the web-weavers (pooled data for all hunters vs. web-weavers) (Table 5). Thus, in agroecosystems there seems to be a consistent trend of greater diet breadth of hunters compared to web-weavers regardless of crop type or geographic region investigated.

How do we explain this difference? Web spiders are stationary predators that wait for food to come to them (i.e., 'sit-and-wait' strategy). The prime requirement for the 'sit-and-wait' strategy is a food that moves (Turnbull 1973). A large proportion of web spiders spin aerial webs, with which they filter the aerial plankton (see Kajak 1965; Chacon & Eberhard 1980; Nentwig 1980). Others spin webs adapted to capture walking, crawling, or jumping prey (Turnbull 1973). Most web-weavers depend largely on relatively few prey groups available in high numbers in a particular environment (see Bristowe 1941; Turn-

bull 1960; Nyffeler & Benz 1979, Sunderland et al. 1986; Nentwig 1987; Alderweireldt 1994). In contrast, hunting spiders, by and large, seem to be less restricted in their diet (see Turnbull 1973). Representatives of various hunting spider families (e.g., Oxyopidae, Salticidae, Thomisidae, Lycosidae) have been reported to feed on both moving and motionless prey, which is indicative of a more mobile foraging strategy (see Nyffeler et al. 1990; Jackson & Tarsitano 1993). It is quite possible that the greater diet breadth of the hunting spiders (Table 4) simply reflects their greater opportunities to actively seek out suitable food due to their higher mobility (see Turnbull 1973).

There is observational evidence that hunting spiders can narrow their diet breadth significantly at times when a suitable prey type becomes locally superabundant relative to other prey (see Kiritani et al. 1972; Dean et al. 1987; Nyffeler et al. 1992b, 1994b). Thus, the greater diet breadth observed in the hunters (Table 4) does not necessarily imply that they require a more diverse diet than the web-weavers. It may instead show that they have a better chance of finding suitable food than web-weavers in agroecosystems (Young & Edwards 1990). However, there are exceptions to the rule (Turner & Polis 1979). Several members of the hunter families Thomisidae, Salticidae, Clubionidae, Gnaphosidae and Zo-

dariidae are known to specialize on ants (see Nentwig 1986, 1987).

Most spiders feed on prey that are small relative to their own size (prey length \leq spider length) (Wise 1993). Feeding experiments with a variety of spider species and a model prey (crickets) conducted in the laboratory revealed that the optimal prey length ranges from 50–80% of the spiders' own length (Nentwig 1987). Nentwig's laboratory data are fully supported by observations in the field (Hayes & Lockley 1990; Nyffeler et al. 1987b, c, 1992a). Overall, spider individuals of small size (including large percentages of immatures) numerically dominate the faunas of field crops, and these feed primarily on tiny prey organisms (< 4 mm in length) (LeSar & Unzicker 1978; Young & Edwards 1990; Nyffeler et al. 1994a).

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SCALE-DEPENDENT DISPERSAL AND DISTRIBUTION PATTERNS OF SPIDERS IN AGRICULTURAL SYSTEMS: A REVIEW

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ABSTRACT. A conceptual framework is presented for the study of the factors affecting the distribution, dispersal and abundance of spiders in agricultural systems. It is useful to consider how factors operate at three levels of a spatial hierarchy, namely micro-habitat, habitat and landscape. The size and distribution of spider populations are determined by factors influencing survival, reproduction and dispersal. Modes of dispersal vary in terms of the efficiency of sampling new habitats and the level of risk. A literature survey of proximal factors (micro-climate, habitat structure, disturbance, prey availability, predation, and territoriality) affecting micro-habitat usage by spiders showed that the relative importance of these factors varied according to spider species. Spider abundance and diversity were found, in general, to be positively correlated with environmental diversity at different spatial scales. Within-field habitat diversifications were found to be more effective in increasing spider populations when interspersed throughout the crop (e.g., polycultures and reduced tillage) than when spatially segregated (e.g., strip management). Two approaches (modeling and experimental) to studying the effects of landscape level phenomena on spider distribution and abundance are discussed. Manipulation of habitats at the edge of fields has not, in the main, resulted in increased spider density within fields. Opportunities were identified for increasing regional populations of spiders, and optimizing pest control, by management of the annual shift in the crop mosaic to maximize spider transfer rates from senescing crops to young crops.

Spiders are ubiquitous predators in terrestrial ecosystems and they have a substantial presence in the agricultural landscape. Species distributions of spiders in various agricultural habitats provide strong evidence that those assemblages are not just randomly collected from the local species pool (Topping & Lövei 1997). Spider diversity varies from being impoverished under intensive culture (Nyffeler et al. 1994) to being, under favorable agricultural management, even greater than in natural habitats (Toft 1989). Agricultural systems are, however, characterized by a relatively small number of highly dispersive dominant agrobiont species, which thrive under disturbed conditions (Luczak 1979). The potential role of spiders in controlling pest populations in agriculture has already been reviewed (Riechert & Lockley 1984; Nyffeler & Benz 1987). Here we depart from the proposition that spi-

ders are useful components of agroecosystems. Our aims here are to determine, from the literature, how spiders are distributed in agricultural systems, to discover the factors which bring about the observed distributions, and to assess whether it might be feasible to manipulate some of these factors to increase the abundance and effectiveness of spider populations as antagonists of pests.

For the discussion of the different factors that influence spider distribution it may be useful to consider the distribution patterns in relation to three nested scales (Wiens 1989; Juhász-Nagy 1992): the *micro-habitat* (e.g., a weedy patch within a field, bare ground between rows of crop plants, or the air space between foliage), the *habitat* (e.g., the whole crop, the adjacent hedge, or an abandoned field), which comprises a collection of micro-habitats, and the *landscape*, which comprises

a collection of habitats. For each scale, we will review dispersal modes, specific factors and farming practices that are relevant to the given level.

MICRO-HABITAT SCALE

Selection of micro-habitat by individual spiders is likely to be in relation to a specific biological need or collection of needs or may reflect avoidance of some factor, such as interspecific encounters (Post & Riechert 1977). The spider may, for example, assess a micro-habitat as a potential web site, oviposition site, overwintering site or as a safe haven from predators during the inactive phase of a diel cycle. Harsh physical conditions are common in agricultural habitats and the spider may need to seek temporary refuge in a favorable micro-habitat in order to maintain its physiological integrity. From this it follows that individuals of any spider population are harbored by specific micro-habitats which might vary over time, according to the current needs of the individuals.

The numbers of spiders to be found, at any instant of time, in each of the micro-habitats are determined by site selection (immigration into the micro-habitats), site-related rates of survival and reproduction (Sunderland & Topping 1993), and site abandonment (Gillespie & Caraco 1987) which, in turn, are determined by various abiotic and biotic factors. Studies aimed at the examination of specific factors can be useful in devising agricultural practices which, typically acting at the habitat scale, might create an improved quality and distribution of micro-habitats for the enhancement of natural enemies.

Abiotic factors.—Structural complexity is usually determined by the vegetation. It provides support for webs and its degree of complexity has a bearing on the costs of exploration and web building (Zschokke 1996). The differential preference of spider species for various structural features can be demonstrated by the strong relationship between structure and the richness and density of spider assemblages (Rypstra & Carter 1995). Manipulations of shrub and tree structure were found to influence spider species diversity and abundance (Hatley & MacMahon 1980). Bultman & Uetz (1982) separated the effects of forest litter as a nutritional base for spider prey from its role as a spatially com-

plex substrate by the use of artificial leaves. Web-builders were more abundant in structured artificial litter but hunting spiders preferred prey-rich natural litter. Other studies employing artificial micro-habitat structures showed that salticids preferred open geometries whilst theridiids selected dense ones (Robinson 1981). Web-builders are not entirely reliant on vegetation, and irregular ground surface features have also been found to meet the requirements of some species. Depressions in the soil of arable fields, for example, are attractive web sites for some linyphiids, and species segregate in relation to the diameter of such depressions (Alderweireldt 1994; Samu et al. 1996). Preference for different structures is also a size related phenomenon. Field data by Gunnarsson (1992) suggested a relationship between spider mean size and vegetation fractal dimension within a habitat, while Riechert (1974) observed change in the structural needs with growth within one species.

Although micro-climate and structure are often correlated (Cady 1984), manipulative experiments have been carried out in an attempt to separate the two factors. Such experiments demonstrated the strong effect of micro-climate: web-site selection occurred in relation to humidity for araneid, tetragnathid and linyphiid spiders (Enders 1977; Gillespie 1987; Samu et al. 1996) and in relation to temperature for the funnel web spider, *Agelenopsis aperta* (Riechert 1985).

Web destruction is often a precursor to web-site abandonment (Hodge 1987). Some micro-habitats may be more prone than others to destructive forces that endanger the web, such as foraging animals and meteorological factors (Enders 1976). Agrobiont species can cope with disturbances by life-history strategies compatible with disturbance patterns (Toft 1989; Samu et al. 1998) and by their high dispersal power. Mobility gives spiders the flexibility to vacate a locally disturbed area and re-invade later. This contrasts with many of their intra-guild competitors, such as carabid and staphylinid beetles, which often have eggs, larvae and pupae in earthen cells highly vulnerable to mechanical disturbance (Sunderland et al. 1996).

Biotic factors.—Cues from prey can (but do not always) play a role in micro-habitat selection and retention. The cues may be vi-

brational (Pasquet et al. 1994), olfactory (Riechert 1985) or visual (Persons & Uetz 1996). The relative importance of these cues varies with species, but Persons & Uetz (1997b) found visual cues to be the most significant for the wolf spider *Schizocosa ocreata*. Many authors (Gillespie 1987; Weyman & Jepson 1994) have reported spiders (belonging to a range of families) to have shorter residence times in micro-habitats where prey is scarce compared with sites where food is abundant. Riechert (1984) showed that if prey was experimentally supplemented in a poor quality web site of *Agelenopsis aperta*, the web owner made more effort to defend its web in territorial disputes. However, often weak or no relationship was observed between site quality and the tenacity of spiders to web-sites. In such cases spiders were demonstrated to follow a fixed probability random leaving strategy (Vollrath & Houston 1986; Persons & Uetz 1997a). An important factor affecting web-site tenacity and responsiveness to prey availability is the energetic cost of web construction, which varies between spider families (Janetos 1982).

A micro-habitat chosen by a spider can act as a refuge from its own natural enemies. In predator exclusion experiments, Gunnarsson (1996) demonstrated that, in the presence of bird predators, the abundance and mean size of spiders were greater on spruce branches where a high needle density provided a refuge from predation. Intraguild predation and cannibalism might affect micro-habitat selection as well. After spiders have reproduced, spatial separation of parents and offspring is often recorded, and this may be a mechanism to reduce cannibalism. Some species of adult lycosid, for example, move horizontally to occupy micro-habitats away from their offspring (Edgar 1971; Greenstone 1983), whilst age-specific vertical migration in *Clubiona phragmitis* may serve the same purpose (Nentwig 1982).

Spider territoriality may be generally uncommon (Wise 1993), but cases are known where agonistic interactions lead to spacing out of the spider population (Riechert 1981; Marshall 1995). In other instances, intra- and interspecific contests for webs and web-sites were observed frequently, without obvious influence on spider aggregation in a micro-habitat. Intraspecific contests between adult fe-

male *Lepthyphantes tenuis* for webs constructed in hollows in the earth of a wheat field were observed regularly (Samu et al. 1996), and they resulted in departure of more than 30% of web-owners from the web-site. An opposite trend can occur amongst less aggressive spiders, where a reduction in web construction costs can be obtained by attaching webs to each other, as was recorded for *Zygiella x-notata* (Leborgne & Pasquet 1987), and *Hypochilus thorelli* (Hodge & Storfer Isser 1997). Various degrees of communality are known in the Araneae, and this has concomitant implications for micro-habitat usage (Rypstra 1986; Hodge & Uetz 1995).

HABITAT SCALE

Habitats are comprised of a number of micro-habitats within a delimited area. Animals which move from one micro-habitat to another within a habitat can usually do so by low-risk dispersal modes. Agricultural fields with their artificial homogenous vegetation can typically be viewed as habitats.

Dispersal within habitats.—Micro-habitat relocations within a habitat are part of the foraging strategy of actively hunting spiders (Ford 1978), but abandonment of web-sites can occur with high frequency in web spiders as well (Samu et al. 1996). To change micro-habitat, walking over the ground (*cursorial dispersal*) is relatively low-risk, as the spider can withdraw rapidly if it accidentally enters inimical territory. However, in extreme environments, even short distance movements, such as within-habitat web-relocation, can significantly increase mortality in a desert widow spider (Lubin et al. 1993). Increased daily movement rates had similar effects for a wolf spider species. In a tidal flood area *Pardosa lapidicina* migrates back and forth with the tides, and the mortality of the population in this habitat was higher than in a nearby salt marsh habitat where the animals moved less (Morse 1997). Cursorial movement could be ineffective for moving across or into large areas of monoculture (Thomas et al. 1990). An alternative dispersal mode is that of "rigging." This entails the spider climbing to the top of the vegetation, letting out strands of silk which fall onto the top of the canopy, then running along the silken line for a few meters and then repeating the process. It is likely to be relatively low-risk and is intermediate be-

tween aerial and cursorial dispersal in terms of habitat sampling rate.

Farming practices.—Many farming operations result in major habitat-scale disturbance for spiders. Harvesting, plowing, pesticide spraying and forest clearcutting are likely to affect most micro-habitats within a given habitat; and they are known to cause severe reductions in spider populations (Nyffeler et al. 1994; Thomas & Jepson 1997). Conversely, disturbances of intermediate strength and frequency may actually increase the diversity of a spider community (Johnson 1995). This effect may operate by increasing the diversity of micro-habitats within a habitat. Another type of diversification might be achieved through the selection of appropriate farming practices which alter vegetation/structure in areas within habitats (fields) that are either spatially segregated (e.g., strip farming) or fully interspersed (e.g., intercropped polycultures, mulching).

Interspersed diversification is frequently attained by planting multiple crop species in one field. This in a number of instances resulted in spider densities greater than those found in monocultures, and an associated suppression of pest species (Letourneau & Altieri 1983; Coderre et al. 1989; Coll & Bottrell 1995). *Lycosid* abundance, for instance, was increased; and corn borer (*Ostrinia furnacalis*) decreased, in peanut intercropped with maize, compared with monocultures (Altieri 1994). Reduced-tillage systems often provide a diversification of interspersed micro-habitats by engendering a rough or heterogeneous soil surface, plus structural complexity in the form of plant residues conserved from previous-year crops (House & Stinner 1983; Clark et al. 1993; Robertson et al. 1994). Other authors (Thornhill 1983; Alderweireldt 1994; Samu et al. 1996) have experimentally demonstrated that linyphiid density can be increased by creating depressions in the surface of arable soils. Clover, as a living mulch (Altieri et al. 1985), and mulches experimentally applied to a garden system (Riechert & Bishop 1990) have been found to increase spider densities significantly, probably by simultaneous effects on structure, micro-climate and prey availability (see above).

Strip management contributes to micro-habitat diversification within crops, but the spatial separation of micro-habitats is greater

than for interspersed treatments. In a Swiss orchard, the density of spiders and their webs on the apple trees was greater in plots where weeds had been planted in strips below the trees, than in weed-free control plots (Wyss et al. 1995). However, in many cases, spider density on and under crop plants is unaffected by strip management (Nentwig 1989; Riechert & Bishop 1990; Samu et al. 1997), perhaps because spiders aggregate in the favorable micro-habitats (such as weed and flower strips) and do not disperse out onto the crop plants.

LANDSCAPE SCALE

The distribution of spiders is least studied at the landscape scale. This is mostly because it is extremely labor intensive to obtain even a coarse picture of spider distribution over a large area. To study the effect of landscape level phenomena on spider distribution two approaches are possible. One is to model landscape scale distribution of spiders using information on the biology of specific species and incorporate that into spatially explicit metapopulation models (Topping & Sunderland 1994b; Halley et al. 1996; Topping, this volume). The other approach is to select smaller scale landscape fragments, a meaningful subset of landscape structures such as a field and its margin, to experimentally study the distribution and movement of spider populations.

Dispersal.—For both above-mentioned research strategies, knowledge of the scale-dependent dispersal of spiders is essential. In fact, Topping's (1997) simulation model appeared to be more sensitive to assumptions about dispersal than to field size or timing of agricultural operations. Spiders can vary dispersal modes, such as cursorial movement, rigging or ballooning, by applying the most effective mode for the given scale of movement, although not all dispersal modes are available in each stage or taxon (Plagens 1986). The most efficient dispersal mode at the landscape scale is ballooning (*aerial dispersal*), which provides the individual spider with the potential to sample different widely-separated habitats in a short period of time (Weyman 1993). If it lands in a safe habitat the spider may have the option to re-balloon immediately, sample the new habitat and re-balloon after a short period of time, or it may choose to stay. As far as is known, the desti-

nation of the aeronaut is determined purely by meteorological factors (Bishop 1990; Thomas 1996). It is, therefore, a high-risk activity; individuals which land at unfavorable destination areas will not be able to reproduce, thus these places act as a reproductive sink (Meijer 1977; Crawford et al. 1995).

Farming practices.—At the landscape scale the effect of basic landscape structure (size and distribution of different habitat types, e.g., fields) and the cumulative impact of field-scale farming practices, (including their timing and distribution), are of primary interest. Root's "enemies hypothesis" (Root 1973), which predicts generalist and specialist natural enemies to be more abundant in diversified agricultural systems, was tested by spatially explicit models at the landscape scale. The maintenance of grass habitats that are not demolished by crop rotation (Topping & Sunderland 1994b) and the presence of set-aside fields (Topping & Sunderland 1994a) significantly increased the viability of the modeled *Lepthyphantes tenuis* metapopulation (Topping 1997). In a simulated linear landscape the inclusion of small amounts of grassland considerably increased overall spider population sizes (Halley et al. 1996). These models were also useful at pointing out the importance of the pattern and timing of destructive agricultural practices. Crop rotation was generally detrimental, but the re-scheduling of plowing could decrease this negative effect on spiders (Topping & Sunderland 1994b).

Using the experimental approach many attempts have been made to increase the abundance of natural enemies in field habitats by manipulation of habitats at the edges of fields. In the majority of such studies (including soybean, cereals and orchards), increases in spider densities at the edges were not translated into increases in the fields themselves, and especially in the centers of large fields (Altieri & Schmidt 1986; Alderweireldt 1989; Kemp & Barrett 1989; Dennis & Fry 1992; Kromp & Steinberger 1992; Altieri 1994; Vangsgaard 1996; Tóth & Kiss 1997). Landscape fragments studied by transect sampling show this phenomenon as the 'edge effect.' Edges are often considered as distinct ecological systems, ecotones, where the local fauna consist of species specific to the ecotone, and a mixture of the two neighboring faunas which

overlap there. The width of the overlap was typically not found to be greater than a few meters for farmland and forest spiders (Bedford & Usher 1994; Downie et al. 1996). Between wheat and various grassy areas the penetration of spiders into neighboring habitats was also limited (Duelli et al. 1990; Kajak & Lukaszewicz 1994). For spiders the absence of certain species from specific habitats is usually due to the lack of habitat suitability, rather than a limitation of dispersal capacity. Bishop & Riechert (1990) found that about half of the spider species found in a garden system were not found in nearby habitats, but arrived by long-distance migration.

Larger scale landscape models suggest that the maintenance of habitat diversity and preserve areas are important for the subsistence of spider metapopulations. On the other hand, smaller scale experimental studies reveal the overriding importance of within field habitat quality. Perhaps these two phenomena could be combined by finding ways to provide "time-specific habitat diversity," such that natural enemy populations build up in favorable non-crop habitats and micro-habitats initially, but are forced to transfer to crop plants (at a time when pests start their increase) by strategically timed destruction of the favorable non-crop habitats. It will be a challenge to develop practical management systems to achieve these goals. Large numbers of natural enemies do, however, emigrate from senescing crops (Whitcomb & Bell 1964); and, since the various crop species in a landscape tend to senesce asynchronously, there is an opportunity to manage the annual shift in the crop mosaic to maximize transfer rates of beneficials from senescing crops to young crops (Burel & Baudry 1995).

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SPIDER PREDATION: HOW AND WHY WE STUDY IT

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ABSTRACT. Predation is of great ecological, evolutionary and behavioral interest. For our present purposes the primary reason for studying it is to determine the role of spiders in suppressing pest populations. Research approaches have included laboratory studies of preference, feeding rate, and fitness; direct observation of predation events or accumulations of prey carcasses; gut analysis; and field experiments. Laboratory studies provide some uniquely useful kinds of information but cannot give reliable indications of the “biological control potential” of spiders against a given pest. Direct observation can be powerful; it has provided the best data on dietary range and predation rates in the field. Gut analytical methods include the use of radionuclides, electrophoresis, chromatography and serology. Serological techniques are preferred: antibodies can be made specific down to the level of prey stage or instar, and assays are simple, sensitive, and reliable. They can determine the relative importance of different predator species, and may be the most efficient methods to document predation on eggs. Problems in quantitation remain. Field experiments have demonstrated unequivocally that spiders can effectively reduce pest populations and the crop damage they cause.

Spiders are ubiquitous in terrestrial ecosystems and abundant in both natural and agricultural habitats (Dondale 1970; Turnbull 1973; Nyffeler & Benz 1987). They also have a suite of adaptations that enable them to wait out periods of low prey abundance rather than dispersing like some other groups of arthropod predators (Ford 1977; Greenstone & Bennett 1980). It has therefore been assumed that spiders play a major role in suppressing insect pest populations (Riechert & Lockley 1984; Young & Edwards 1990). However their small size, cryptic habit, and mode of feeding have made it difficult to determine whether this is so (Kiritani & Dempster 1973; Stuart & Greenstone 1990).

HOW PREDATION IS STUDIED

Predation data can be obtained by four means: laboratory feeding studies, direct observation in the field, gut analysis, and experimental field manipulations.

Laboratory studies.—There is a large literature in agroecosystem entomology and arachnology describing feeding trials of individual predators confined with prey in small containers in order to determine their “predatory potential.” For spiders this approach is problematic since most are oligophagous or polyphagous (Nentwig 1986), and neither choose nor survive and reproduce well on single-species diets (Miyashita 1968; Van Dyke

& Lowrie 1975; Hydhorn 1976; Greenstone 1979; Lowrie 1987; Uetz et al. 1992; Toft 1996). Another difficulty is our lack of knowledge of the role of environmental variables in predator-prey behavioral interactions.

Web spider feeding trials are least apt to be compromised, because many of the critical environmental and behavioral elements are embodied in the web itself. But hunting spider feeding trials are generally performed in simple open arenas—rarely made more realistic by provisioning plant bouquets (Lingren et al. 1968)—and the spiders are usually starved for a day or even a week (Young 1989a; Punzo 1991; Sadana & Kumari 1991) to increase the likelihood of a result. Since a starved spider in a small, featureless arena is apt to attack any but the most unsuitable (noxious, venomous, too large or too well armored) arthropod placed before it, it is hardly surprising that such spiders usually feed, and sometimes consume large numbers of prey. However, lengthy starvation inflates feeding rates (Toft 1996); furthermore, starvation causes reductions in basal metabolic rate (Anderson 1974), which could change feeding latency or otherwise distort predatory behavior. Since spiders in the field usually consume about one appropriate-sized insect per day (Edgar 1969, 1970; Schaefer 1974; Morse 1979; Nyffeler 1982; Nyffeler & Benz 1988a, b; Nyffeler et

Table 1.—Studies in which direct observation was used to determine the spectrum of spider species attacking a pest, pest complex or biological control agent.

Prey	Reference
Acari	
<i>Metatetranychus ulmi</i> (Koch) & <i>Bryobia praetiosa</i> Koch	Chant 1956
Lepidoptera	
<i>Helicoverpa zea</i> (Boddie) & <i>Heliothis virescens</i> (Fabricius)	Quaintance & Brues 1905 Fletcher & Thomas 1943 Whitcomb & Bell 1964 Whitcomb et al. 1963 Whitcomb 1967
<i>Anticarsia gemmatilis</i> Hübner	Elvin et al. 1983 Godfrey et al. 1989 Gregory et al. 1989
<i>Hyphantria cunea</i> (Drury)	Whitcomb & Tadic 1963
<i>Coleophora parthenica</i> Meyrick	Nuessly & Goeden 1983
Coleoptera	
<i>Diaprepes abbreviatus</i> (L.)	Richman et al. 1983a,b
<i>Ips</i> and <i>Dendroctonus</i> spp.	Jennings & Pase 1975, 1986
Heteroptera	
<i>Pseudatomoscelis seriatus</i> (Reuter)	Dean et al. 1987

al. 1987a, 1992a), starved spiders may not behave normally (but see Bilde & Toft 1998). These same objections apply when more than one prey type is offered simultaneously to determine preferences (e.g., Provencher & Coderre 1987; Gillebeau & All 1989). Also, apparent preferences may be perversely misleading because a less preferred, even patently unpalatable prey species may, in combination with others, provide greater fitness than a pure diet of a preferred species (Toft 1995, 1996).

Space does not permit a discussion of the numerous laboratory studies to generate spider functional response curves, but the same objections apply. The non-congruence of field and laboratory functional response data for one intensively studied insect predator (O'Neill 1997) should give us pause in contemplating the initiation of such lab studies.

Other feeding questions are well suited to laboratory study. Sunderland et al. (1986) determined escape rates of aphids from occupied linyphiid webs under varying conditions of falling frequency, aphid stage and spider satiation, necessary for converting field web density estimates into predation potential. Edgar (1969, 1970), Kiritani et al. (1972), Nyffeler & Benz (1988b) and Nyffeler et al.

(1987a, b) determined the time during which prey items were carried and fed upon by spiders, a parameter needed to convert field observations on feeding to predation rates (see also below). A general case for which laboratory studies are defensible is where one needs to know about preferences of highly stenophagous predators (e.g., Morse 1984; Li & Jackson 1996).

Direct observation.—Our most extensive data on spider prey spectra, prey preferences and predation rates are derived from extensive field observations of spiders feeding and from the identification of prey carcasses taken from spiders' webs.

Prey spectrum. These studies focus on either the spiders attacking a particular pest or pest complex, or the prey spectrum of particular guilds of spiders. Table 1 lists studies of the first kind. In a paper on bollworm predation, Whitcomb (1967) pioneered the placement of eggs or larvae at regularly spaced stations to facilitate data collection, a method later used for studies of the velvetbean caterpillar (Elvin et al. 1983; Godfrey et al. 1989) and sugarcane rootstalk borer (Richman et al. 1983a,b). Whitcomb & Tadic (1963) surveyed spider predators of the fall webworm, a task facilitated by the arresting power of the webs

Table 2.—Rates at which field observations of feeding rate by hunting spiders have been collected by human observers. *Best estimate if investigators did not record exact number of hours. **Events/person-hour; in all cases only one author made observations (see Acknowledgments).

Spider species	Habitat	Events	Hours*	Rate**	Reference
<i>Phidippus audax</i>	cotton	58	10	5.80	Young 1989c
<i>Oxyopes salticus</i>	cotton	48	11.25	4.27	Lockley & Young 1987
<i>Peucetia viridans</i>	woolly croton	68	25.5	2.67	Nyffeler et al. 1987b
<i>Lycosa anteleucana</i>	cotton	147	91.4	1.61	Hayes & Lockley 1990
<i>Dolomedes triton</i>	ponds	625	~400	1.56	Zimmermann & Spence 1989
<i>Pardosa</i> spp.	wheat	106	104.5	1.01	Nyffeler & Benz 1988b
<i>Oxyopes salticus</i>	cotton	64	85	0.75	Nyffeler et al. 1987a
<i>Phidippus audax</i>	woolly croton	19	25.5	0.75	Dean et al. 1987
<i>Pardosa ramulosa</i>	salt marsh	32	~50	0.64	Greenstone 1976
<i>Oxyopes salticus</i>	cotton	63	108	0.58	Nyffeler et al. 1992b
<i>Misumenops celer</i>	woolly croton	11	25.5	0.43	Dean et al. 1987
<i>Metaphidippus galathea</i>	woolly croton	9	25.5	0.35	Dean et al. 1987
<i>Peucetia viridans</i>	cotton	31	108	0.29	Nyffeler et al. 1992b
<i>Peucetia viridans</i>	cotton	25	85	0.29	Nyffeler et al. 1987b
<i>Misumena calycina</i>	old field	16	79.3	0.20	Morse 1979
<i>Pardosa milvina</i>	cotton	14	91.4	0.15	Hayes & Lockley 1990
<i>Pisaurina mira</i>	cotton	12	~300	0.04	Young 1989b
<i>Phidippus johnsoni</i>	various	33	~3,000	0.01	Jackson 1977

of the prey, which collected the spiders for the investigators' perusal.

The guild-centered prey spectrum literature comprises thousands of person-hours of direct observation (see Nyffeler 1999, this volume, for a thorough review and analysis). Hunting spiders pose the biggest challenge because they are less easily found and do not leave the carcasses of their prey where they can be identified and counted. Thirteen studies for which one can estimate the rate of discovery of hunting spider predation events by a human observer are summarized in Table 2. They reveal a surprising range, from about 0.01 to almost 6 events/person-hour of observation; rates for one species in cotton (*Oxyopes salticus*) varied seven-fold. These data demonstrate that direct observation can sometimes be an efficient way to learn about the prey spectrum of hunting spiders, and may enable the investigator to assess the effort likely to be involved in such an undertaking.

Predation rates: Predation rates for web spiders can be obtained directly from web densities and counts of prey carcasses in webs or in sticky traps, provided prey escape probabilities are determined; and an advantage of using traps is that they can obviate the need to work at night (Sunderland et al. 1986). Determining predation rates of hunting spiders

by direct observation requires ingenuity; an approach was outlined by Edgar (1969, 1970) and formalized by Nyffeler & Benz (1988b). Their formula contains an estimate of the hours per day spent hunting. Such an estimate is implicit in all predation rate estimates, and must be stated explicitly if the investigator limits the time during which data are taken (Jmhasly & Nentwig 1995). Published predation rates for web and hunting spiders, variously expressed, are presented in Table 3.

Rates for individual spider species and species complexes suggest relatively low proportions of pest populations being destroyed, but one must remember that spiders constitute an assemblage of species that may, in aggregate, exert effective control (Riechert & Bishop 1990; Riechert & Lawrence 1997). Furthermore, spiders kill many more insects than they consume (see Sunderland 1999, this volume). Finally, in conjunction with parasitoids, pathogens, and other polyphagous predators, spiders may tip the balance in biological control.

Intraguild predation: Prey spectrum studies reveal that some spiders consume large numbers of beneficial arthropods, including other spiders and parasitic and predatory Hymenoptera and Diptera (see Hodge 1999, this volume); most notorious is the green lynx spider, *Peucetia viridans* (Turner 1979; Randall 1982;

Table 3.—Spider predation rates and prey population impacts derived by direct observation. *Data collection restricted to hours of daylight. **Based on calculation from raw data in Edgar 1969.

Species or Complex	Rate	Impact	Reference
Web Spiders			
All foliage web spiders	0.2–1.2 × 10 ⁶ insects/ha/year		Nyffeler (1982)
	0.2–1.2 kg insects/ha/year		
Araneidae only	38 insects/m ² /day		
	150 fresh kg insects/ha/year		
<i>Araneus</i> spp.	12 insects/m ² /day		Kajak 1965
Linyphiidae, Araneidae & Tetragnathidae	3.5–5.8 prey /m ² /9 h day*		Jmhasly & Nentwig 1995
Linyphiidae only	1.5–1.7 aphids/m ² /9 h*	4% of aphid population	
Linyphiidae	0.023–31.2 aphids/m ² /day		Sunderland et al. 1986
	105.6 aphids/m ² /season		
Micryphantidae	42 insects/m ² /day	2% of aphid population	Nyffeler & Benz 1988a
	20 aphids/m ² /day		
Hunting Spiders			
<i>Pardosa</i> spp.	~1.3 insect/day		Nyffeler & Benz 1988b
	2 aphids/m ² /week		
<i>Pardosa lugubris</i>	0.8 insect/day**		Edgar 1969
<i>Pardosa amentata</i>	1.17 insect/day		Edgar 1970
<i>Peucetia viridans</i>	0.25–0.5 insects/day		Nyffeler et al. 1987b
<i>Oxyopes salticus</i>	120,000 insects/ha/week	4.5% of available prey	Nyffeler et al. 1987a
<i>Oxyopes salticus</i>	0.9 insects/day	15–18% avail. flea-hoppers	Nyffeler et al. 1992a
<i>Phidippus audax</i>		5% of available prey	Young 1989c

Nyffeler et al. 1987b). Randall (1982) asserted that the green lynx is “counterproductive” as a biological control agent, but the only sure way to determine this would be to study the agroecosystem in its presence and absence. Louda (1982) performed just such a study of predation by *P. viridans* in a natural system and found that its net effect was beneficial to plants.

Gut analysis.—Identifying and quantifying prey remains in the gut are the first steps in determining spider predation rates (Sunderland 1996). However, because spiders are liquid feeders and the remains of several meals may be found concurrently, this presents formidable technical problems (Stuart & Greenstone 1990).

Radionuclides: Breene et al. (1988) showed that when mosquito larvae irradiated with ³²P were made available to three amphibious spi-

der species in simulated ponds, spider feeding could be documented by acquired radioactivity. Similar approaches were used to document spider predation on moth eggs and larvae (Buschman et al. 1977; McCarty et al. 1980; McDaniel & Sterling 1979; Elvin et al. 1983; Godfrey et al. 1989). To use this approach in the field, one must label and release large numbers of potential prey and then determine the proportion of total prey that are labeled. One must also assume that the released animals and those of the natural population are equally susceptible to predation, and that radioactivity is not being made available to the spiders by other routes. Finally, this approach would be difficult to employ given environmental concerns and regulations (Elvin et al. 1983); besides, there are better alternatives (below).

Chromatography: In a unique application,

Putnam (1967) used paper chromatography to detect the pigments of mites that had been consumed by spiders.

Electrophoresis: Gel electrophoresis of prey allozymes has been used for insect and mite gut analysis but not yet for spider gut analysis. One must pay serious attention to the choice of enzyme system and gel medium, and be a competent bench scientist (Solomon et al. 1996). If it could be made to work, an advantage would be relative economy and, with luck, the ability to distinguish a wide range of prey species with a single analytical system.

Nucleic acid probes: Probes employing species-specific DNA sequences have been used to diagnose a number of arthropod interspecific interactions, including pathogen host and parasitoid host (Greenstone & Edwards 1998), and could, in principle, be used to identify prey remains in a spider's gut.

Serology: Vertebrate antibodies have been used for spider gut analysis for 35 years (Loughton et al. 1963). I have recently reviewed this approach (Greenstone 1996) and shall here emphasize just three points. First, these are proven technologies with stable, reproducible protocols. Second, assay technology is getting cheaper and simpler; and ELISA, which requires expensive equipment, could be replaced by the immunodot (Stuart & Greenstone 1990; Greenstone & Trowell 1994; Agustí in press). Finally, any level of prey specificity is achievable, down to stage and even instar (Ragsdale et al. 1981; Greenstone & Morgan 1989; Greenstone & Trowell 1994; Goodman et al. 1997). Although most directly achieved by monoclonal antibody technology, the same specificities might be achieved more cheaply by affinity chromatography of conventional antisera (Greenstone 1996).

Serological assays have been used to study spider predation on all manner of arthropod prey (Greenstone 1996). They are particularly useful for studying oophagy, a poorly documented phenomenon because of the small size and cryptic habit of eggs and short spider handling times (Nyffeler et al. 1990). For example, a single monoclonal antibody has revealed the extent of bollworm egg predation by two *Cheiracanthium* species in India and North America (Sigsgaard 1996; Ruberson & Greenstone 1998).

Two problems in quantitating serological data remain. First, predators differ in digestive rates and are therefore differentially likely to contain detectable remains of a prey item at any interval post-feeding. Weighting factors, based on temperature-dependent detectabilities, are necessary to determine the relative importance of different predator species. Maximum detectability intervals (Sunderland et al. 1987) and detectability half-lives (Greenstone & Hunt 1993; Agustí in press) have been proposed as weighting factors. Second, due to the extraordinary sensitivity of contemporary assays, one generally cannot know the number of prey items represented by a serological positive (Greenstone 1996). If one assumes that the number of prey contained in any given predator gut is a Poisson variate, then the proportion of negatives can be used as the zero class to calculate the mean number of prey individuals per gut (Nakamura & Nakamura 1977; Greenstone 1979; Lister et al. 1987). Since Poisson assumptions may not always be met, the model needs to be tested. Other models have been suggested by Ashby (1974), Sunderland & Sutton (1980), and Sopp et al. (1992).

Field experiments.—Direct evidence for the effectiveness of spiders in biological control comes from field experiments in which spider numbers are manipulated and the resultant pest populations and attendant crop damage are compared to those in controls.

Mansour et al. (1980) removed all of the spiders from half of a sample of apple trees in an abandoned orchard and then infested them with Egyptian cotton leafworm egg masses. After five days, damage to egg masses was significantly greater; and larval populations and leaf feeding damage were significantly lower on the controls. Analogous experiments were performed with the same insect on cotton (Mansour 1987) and a scale insect on citrus (Mansour & Whitcomb 1986), with similar results.

Itô et al. (1962) used heptachlor to reduce spider numbers in a rice ecosystem. Spider densities were lower and planthopper and leafhopper densities and population growth rates were greater where plots had been sprayed. In a northern California rice ecosystem, Orazé & Grigarick (1989) used floating rings with sticky tops to manipulate the numbers of *Pardosa ramulosa* within. Rings with

higher spider densities had significantly reduced densities of the aster leafhopper.

Carter & Rypstra (1995) added artificial web sites (crates) and an inoculum of *Achaearanea tepidariorum* to some soybean plots and removed all spiders and uninhabited webs from others. Crates increased spider density, which was significantly correlated positively with insects killed and negatively with leaf area damaged.

Riechert & Bishop (1990) increased the hospitability of a vegetable garden ecosystem by adding mulch, which significantly increased spider density and decreased pest densities and plant damage. After spider removal, the mulch treatments were no longer different from bare ground controls. Riechert & Lawrence (1997) manipulated numbers of the entire spider assemblage and also of four individual species (an abundant small lycosid and linyphiid and less abundant but large lycosid and araneid), in an old field ecosystem. The entire assemblage significantly reduced insect herbivore numbers relative to spider removal controls, but individually the abundant small species could also significantly reduce the densities of some insect taxa.

CONCLUSIONS

All four approaches to studying spider predation have some value, but laboratory feeding studies are only useful in selected cases; before succumbing to the temptation to perform them, one should ask whether the resulting data are likely to be informative (Howell & Pienkowski 1971). Direct observation is a powerful tool that will continue to provide useful information on prey spectrum and feeding rates. Serological gut analysis is the most efficient and least disruptive method available for gathering large-scale spider predation data on selected prey species. Experimental field manipulations provide the most powerful demonstrations of the efficacy of spider species and assemblages as biological control agents, and they can also serve as realistic trials for proposed management approaches (e.g., Riechert & Bishop 1990).

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SPIDER COMPETITION IN STRUCTURALLY SIMPLE ECOSYSTEMS

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ABSTRACT. Spider competition has long been an elusive phenomenon for ecological study. Because most spiders are generalist predators, they are predicted to overlap in resource use wherever they overlap in space use and activity periods. However, despite this obvious potential for competition, the empirical evidence for competition has been weak. Spider competition could potentially limit densities in agricultural ecosystems, which would limit their effectiveness as biological control agents. We summarize the results of five studies in a type of ecosystem which may be considered to be analogous to row crops in both the physiognomy of vegetation and cyclic disturbance regimes, namely, wetlands. In addition, we summarize the results of our own work in a soybean ecosystem.

Interspecific competition occurs whenever the availability of a limiting resource is reduced by the presence of two or more species which rely on the same resource. Species which are more efficient or aggressive in resource use are predicted to prevail over other species. Exploitative competition occurs when one species has a negative effect on individuals and/or populations of another because it is more efficient at using a limiting resource. However, competitive interactions can also be behavioral, such as when one species alters the space use or feeding behavior of a second species, resulting in a reduction in access to important resources by the second species. This is termed 'interference competition'.

It seems intuitively obvious that resource limitation by the action of other species should be an important phenomenon influencing the success of species populations and, ultimately, community structure. However, just how prevalent and significant competition is has been the subject of extensive and often contentious debate for decades (Strong et al. 1984). One of the key assumptions in competition theory is that one of the species in a community is better at exploiting some limiting resource, and does so to the detriment of

other species. Because both resource availability and population densities of the competitors may vary for reasons that have nothing to do with the activities of the competing species, competition may not be a persistent phenomenon. Also, no two species will ever use the same resource in precisely the same way. Even small variations in resource exploitation strategies will reduce the intensity of competitive interactions.

The most generally accepted paradigm in spider ecology is that spiders are food-limited generalist predators of arthropods, particularly insects. Spiders rarely specialize in specific prey taxa; however, the prey spectrum of any spider species population will never be a perfect reflection of all potential prey in their environment. Some prey will either be rejected as too risky because they possess defenses, or will not be encountered at all as they are not active in the same places at the same times of the day as the spiders are foraging. However, given these constraints on prey use, there is still the potential for different species of generalist predators like spiders to share prey taxa (Nyffeler & Sterling 1994). Intraspecific competition would be predicted to be the strongest, given that resource use should overlap 100% within a single species age/size class. However, because many spiders are territorial, and potentially cannibalistic, they will tend to be self-limiting. Because of these population

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regulation mechanisms, spider densities are predicted to rarely be high enough to set the stage for density-dependent resource limitation (Riechert 1974).

Evidence for interspecific competition in spiders has been rare enough that it may be viewed as the exception and not the rule (Wise 1993). However, there are similarities among the strongest examples of interspecific competition we found which suggest that competition may be more prevalent in structurally simple ecosystems which exhibit a gradient of habitat structure than those ecosystems which are more uniform and exhibit greater vertical stratification. Examples of structurally simple successional ecosystems are estuaries, wetlands, and an anthropogenic analog, agricultural ecosystems. Early research in spider community ecology documented the fact that early successional habitats had lower spider species diversity when compared to later seral stages nearby (Lowrie 1948; Barnes 1953). In these cases, this relatively low spider species diversity was functionally linked to the relative structural simplicity of the vegetation. The link between vegetation structure and spider species diversity was explicitly tested by Greenstone (1984). This link between structural simplicity and species poverty was extended to the litter layer by Uetz (1979). The link between the structural complexity of habitat and spider species diversity is so well-established as to be a paradigm in spider ecology (Uetz 1991; Wise 1993).

Wetland ecosystems are structurally simple because they are biotically simple. Tidal estuaries, in particular, have few plant species which in turn supports a species poor community of herbivores and predators. In addition, there is an inshore-outshore gradient of the intensity and cycle of disturbance which results from cyclical disturbance by flowing water. Along this disturbance gradient habitat complexity varies from barren soil at the water's edge, to complex vegetation inshore (Cameron 1972; Uetz 1976). Agricultural ecosystems are structurally simple systems by design. Intensive cyclic disturbance regimes in tandem with the mechanized dispersal of seeds are all techniques used to attempt to create landscapes colonized by one species: The crop plant. However, despite the strenuous efforts of agriculturists, many species of plants and animals do colonize agricultural fields.

Because most crop plants have an annual crop cycle, and because of the disturbances inherent in crop management, most invading species of plants and animals are those naturally associated with early successional ecosystems (Wissinger 1997). The evolved ability of these pioneer species to invade and reproduce in a narrow window of time, tolerate abiotic extremes, and benefit from disturbance preadapts them to life in an agricultural field (Luczak 1979).

Spiders are common and often abundant incidental colonists of agricultural ecosystems. Young & Edwards (1990) found that 614 spider species are found in crop systems in North America. Studies of the spiders associated with crops found that the spiders found there are generally not species invading from local natural ecosystems, but those species found in the surrounding agricultural landscape (Duelli et al. 1990; Bishop & Riechert 1990). In our own fields at the Miami University Ecology Research Center in southwestern Ohio we found that the two dominant wolf spider species (*Hogna helluo* (Walckenaer) and *Pardosa milvina* Hentz) are absent from the native forest adjacent to the fields, but common in riparian and pond edge habitats in the area (Marshall & Rypstra unpubl. data).

Araneid competition in a California salt marsh.—Dave Spiller's 1984 study of the competitive interactions between two araneids, *Cyclosa turbinata* (Walckenaer) and *Metepeira grinneli* (Coolidge), in a salt marsh ecosystem near San Francisco remains one of the clearest experimental demonstrations of interspecific competition between spiders to date (Wise 1993). The higher and drier parts of this marsh are dominated by two plant species: *Salicornia pacifica* and *Baccharis Douglasii*. *Salicornia* is a low-growing woody perennial herb, and *Baccharis* a shrub (Cameron 1972). Spiller was motivated to study the potential for competition between these two species by both the high densities achieved by these spiders and the apparent absence of predators. Densities of these spiders are indeed high. In ten 1 × 1 m plots established to study the phenology of the focal species, *Metepeira* densities approximated 1 per m², and *Cyclosa* 10 per m² (Spiller 1984). *Metepeira* was the larger of the two, having approximately twice the body length of *Cyclosa* as an adult (Spiller 1984).

Spiller conducted his experimental studies in replicated 4×1 m plots, with three plots for each removal treatment and three controls. Across these plots the foliage height approximated 1.25 m. Spiller removed *Cyclosa* or *Metepeira* over a six month period and noted the response by the other species in numbers, web height, and fecundity. Spiller found evidence of both exploitative and interference competition in this pair of spiders. Removing the much more common *Cyclosa* resulted in an increase in the body size and fecundity of *Metepeira*. The mechanism to explain this result is the increased foraging success of *Metepeira* in plots free of *Cyclosa*. The much larger *Metepeira*, on the other hand, engaged in interference competition with *Cyclosa*. Both *Cyclosa* densities and web placement were affected by *Metepeira*. *Cyclosa* numbers were higher, and their webs were higher in the vegetation in the *Metepeira* removal plots.

Spiller's findings are significant because they represent clear evidence of how interspecific competition can influence both space use and fitness in spiders. However, it is also revealing that these results come out of a type of terrestrial ecosystem which is structurally simpler than most. The salt marsh ecosystem in which he worked was dominated by two plant species, and this vegetation had a low growth form. In addition, the densities of these two species were high enough that they were likely to have the opportunity to interact.

Wolf spider competition in a German salt marsh.—Schaefer (1972, 1974; summarized in English in Schaefer 1975 and Wise 1993) studied how competition might explain the patterns of space use exhibited by three lycosid species across a shoreline-salt marsh ecotone on a bay of the Baltic Sea near Kiel, Germany. These lycosids were: *Pirata piraticus* (Clerck), *Pardosa purbeckensis* (F.O.P.-Cambridge), and *Pardosa pullata* (Clerck). The *Pirata* and *Pardosa purbeckensis* were more common in the salt marsh, and *Pardosa pullata* was more common on the dry ground fringing the salt marsh. However, all three overlapped in substratum use. *Pirata* was the largest of the three and would opportunistically prey upon the two *Pardosa* spp. Schaefer found that *Pardosa purbeckensis* comprised up to 8.2% of the diet of *Pirata*.

Schaefer conducted density manipulation experiments in the salt marsh as did Spiller

(1984). His treatment consisted of reducing *Pirata* densities by applying insecticide (a ParathionTM spray) to four 10×10 m plots. He had a fifth untreated control plot. The ParathionTM treatment initially eliminated all spiders, however, as *Pirata* was much slower to reinvade the plots than the *Pardosa* spp., its populations were never able to recover from the treatments (as he intended). Additionally, he sprayed the edges of the plots weekly to further limit recolonization by *Pirata* (Schaefer 1974, reported in Wise 1993). Schaefer (1975) reported a significant and impressive reduction in *Pirata* numbers as a result of his manipulations. Mean densities of *Pirata* in the Parathion plots was 2.2 per m^2 , and in the control plot, 14 per m^2 (Schaefer 1975, table 1). On the other hand, both *Pardosa* spp. densities were higher in the Parathion plots than in the control plots (*P. purbeckensis*; Parathion, 9.6 per m^2 , control 8.3 per m^2 ; *P. pullata*; Parathion 3.5 per m^2 , control 2.8 per m^2). Schaefer found no statistically significant increase of *Pardosa* spp. numbers in the Parathion (i.e., *Pirata* removal) plots. As Wise (1993) notes, it is hard to interpret these results in light of the fact that Schaefer had only one control plot. However, it is nonetheless interesting to note that the two *Pardosa* spp. were in higher numbers in the Parathion plots despite the insecticidal application, when *Pirata* numbers were so low.

Schaefer conducted a second experiment in six 2×2 m enclosures in the salt marsh. He had six treatments, with one replicate each (Schaefer 1975). In each he added either each *Pardosa* spp. alone, each alone with *Pirata*, the two *Pardosa* spp. alone together, and all three together. All spiders were added in natural densities (*Pirata*: 2.5 per m^2 , *P. purbeckensis*: 2.0 per m^2 , *P. pullata*: 0.5 per m^2). He found that the mean densities of *P. purbeckensis* were higher in the enclosures where it was alone or with *P. pullata* (9.7 per m^2) than in the two enclosures with *Pirata* or the open control plots (6.5 per m^2). He also found that *P. pullata* was more common in the enclosures where it was alone, or with *P. purbeckensis* only (3.3 per m^2) than in the two enclosures with *Pirata* or in the single open control plot (2.5 per m^2). Based on his statistical analysis Schaefer concluded that he did not have any basis to invoke competition in the patterns he observed. However, in his reanalysis of the

data, Wise (1993) suggests that Schaefer was too conservative in drawing his conclusions and that in fact he had evidence for interspecific competition.

Schaefer found limited, but compelling evidence that the larger *Pirata piraticus* had an impact on numbers of the two *Pardosa* spp. where they co-occurred. This interaction was primarily mediated by predation by *Pirata* on the *Pardosa* spp., as well as presumably some interference interactions. Like the two araneids in Spiller's (1984) study, these combative lycosids lived at relatively high densities in a structurally two-dimensional ecosystem.

Space use by lycosids on the New Jersey shore.—Döbel et al. (1990) examined the relationship between vegetation structure and tidal flooding with spider community structure in a salt marsh near Tuckerton, New Jersey. This study was specifically designed to examine species diversity as a function of habitat structure and disturbance. However, they also uncovered indirect evidence of competition between two lycosid species, *Lycosa modesta* (Keyserling) and *Pardosa littoralis* Banks. This study was entirely correlative, and consisted of a series of D-VAC samples taken in two replicates of four categories of *Spartina* spp. vegetation. On the shore was *S. patens*, a low growth form type of grass with a thick thatch base. Below the mean high water mark were three growth forms of *S. alterniflora*: short, intermediate, and tall. Every two weeks between early May and October they D-VAC'd four sites within each of the eight plots. Each sample was four, 15 sec applications of the D-VAC head to the vegetation. They found that *L. modesta* and *P. littoralis* were the numerically dominant hunting spiders in this salt marsh ecosystem (Döbel et al. 1990). The authors concluded that the patterns they observed for most species were in fact correlated with the architecture of the *Spartina*, the depth of the thatch, and the cycle of tidal disturbance. One exception was for the habitat use patterns of *L. modesta* and *P. littoralis*. *Pardosa littoralis*, alone among the species graphed (Döbel et al. 1990), exhibits a dip in densities in the short form *Spartina*. This is the second of the four successive categories of *Spartina* habitat going from higher to lower elevations. This is noteworthy as all the other species graphed exhibit single peak in abundance across the inshore-outshore gra-

dient. This dip in densities exhibited by *P. littoralis* (to almost zero) corresponds to the single and very pronounced peak in *L. modesta* numbers. The authors note: "...it is likely that the larger (10–12 mm) and more aggressive *L. modesta* simply drives the smaller (6 mm) *P. littoralis* from short-form *S. alternifolia*." (Döbel et al. 1990). Unfortunately, the authors do not detail the basis for their assessment of the temperament of *L. modesta*. However, given the strength of the pattern they observed, it would be well worth an experimental study of the interactions of these two lycosids.

Lycosid competition in a hot springs ecosystem.—John Moeur studied the foraging consequences of competition between two lycosids (*Pirata maculatus* Emerton and *Pardosa altamontis* Chamberlin & Ivie) which live on bluegreen algal mats near hot springs in Serendipity Meadow at Yellowstone National Park (Moeur 1977). The ecosystem Moeur studied consists for the most part of the algal mats, a brine fly (Diptera: Ephydriidae, *Paracoenia turbida*) which feeds on the algae, and the two lycosids which feed on the flies. Through direct observation, Moeur determined that the brine fly *P. turbida* comprised at least half the diet of both spider species (Moeur 1977). He also found that they overlapped broadly in activity periods, although the *Pirata* was more active early and late in the day, and the *Pardosa* was more active near midday (Moeur 1977). Moeur observed agonistic interactions between the two spiders, which led him to investigate the potential for competition between them: "When two meet, the larger spider invariably drives off the smaller, though it rarely kills it. Encounters between equal-sized individuals evoke much leg waving and feints by each animal before one routs the other. After a confrontation lasting a few seconds, *P. maculatus* usually drives away *P. altamontis*." (Moeur 1977, p. 30).

Moeur conducted enclosure experiments in which he tested for the impact of *Pirata* on *Pardosa* survival and fecundity. He constructed five artificial streams 1.22×2.44 m in area. He added vegetation (i.e., algae) from the surrounding hot springs habitats. He set up different ratios of 20 adult female *Pirata* and *Pardosa* in each. These ratios were: 20:0, 15:5, 10:10, 5:15, and 0:20 *Pardosa*:*Pirata*.

Moeur apparently added and removed the *Pardosa* from these systems on a weekly basis, although it is hard to tell from his description of the methods (Moeur 1977). Whatever the details of his methods, he found a clear pattern of reduced *Pardosa* survivorship in enclosures with more *Pirata* (Moeur 1977). He attributes this outcome to interference competition mediated by the agonistic interactions he observed.

Field and lab test for lycosid competition in soybean agroecosystems.—We have been studying the ecology and interactions of two lycosids, *Hogna helluo* (Walckenaer) and *Pardosa milvina* Hentz, in two soybean agroecosystems since 1994. These two spiders seemed to exhibit elements of some of the systems we have reviewed above: A larger, less vagile, and less common species (*Hogna*) which we predicted might engage in interference competition and intraguild predation with the smaller, more vagile, and more common species (*Pardosa*). In the first field season (1994) we recorded both species in high densities. Using a restricted-area search sampling method, we recorded a high of approximately 0.8 *Hogna* per m², and 2.0 *Pardosa* per m² (Marshall & Rypstra in press). We tested for competition in both the field and lab.

Our field studies of competition were conducted in replicated field plots (Marshall et al., unpubl. data). In six, 0.42 ha soybean plots we created eight 6 × 6 m islands of enhanced wolf spider microhabitat using wild bird seed (to increase vegetation) and wheat straw mulch. We enhanced prey availability by adding composted vegetable waste to selected subplots. We had three treatments and a control, repeated for each species (for a total of eight subplots): 1) spiders added, 2) prey attractants added, 3) spiders and prey attractants added, and 4) control. Each two weeks from June to September we added the compost and/or the spiders. We added *Pardosa* and *Hogna* in numbers similar to natural densities we observed in the field (Marshall & Rypstra in press); 25 *Hogna* and 36 *Pardosa* per 36 m² subplot). At the end of the season we censused a third of the area of each subplot using a restricted area search method. We found no significant decrease in *Pardosa* numbers in the *Hogna* addition plots, although these were the lowest *Pardosa* densities we recorded (Marshall et al. unpubl. data). Interestingly,

we collected more *Pardosa* than we added to most plots, but recovered far fewer *Hogna*. This indicates that something was limiting *Hogna* densities, perhaps intraspecific competition. The extremely low densities of *Hogna* when compared to *Pardosa* may also explain the limited evidence for interspecific competition we found.

We also conducted laboratory mesocosm tests for competitive interactions between the two species. We compared the weight gain of eight *Pardosa* held alone to the weight gain of six *Pardosa* in enclosures with a single *Hogna*. We applied a paraffin muzzle to the *Hogna* to prevent them from preying on the *Pardosa*. This was done using a protocol devised by Jerome Rovner (Rovner 1980). These mesocosms were 40 liter aquaria (25 cm × 50 cm × 32 cm). Each aquarium was filled with soil from the soybean fields to a depth of 3.5 cm. One half the soil surface in each aquarium was then covered in 3.5 cm of pine bark mulch. A house plant (*Syngonium podophyllum*), 17–25 cm, high was placed in the mulched half of the tank to offer vertical stratification. The tanks were lit on a 12:12 light: dark cycle by standard fluorescent lights suspended over the tops of the tanks. The *Hogna* were placed in randomly assigned tanks one day before the *Pardosa* were added. *Pardosa* were randomly assigned to treatments, and weighed and placed into their assigned tank. This was done in the early evening; data collection began the following morning and lasted one week. Vestigial-winged fruit flies (*Drosophila melanogaster*) were introduced into the tanks twice during the week as food for the *Pardosa*. The flies were added in sufficient numbers to assure a constant supply of prey. We misted the soil often enough to keep the soil moist. At the end of seven days the spiders were removed from the tanks and weighed.

We found a significant reduction in weight gain by *Pardosa* in the presence of *Hogna*. *Pardosa* alone gained 45.3 ± 10.6 ($\bar{x} \pm 1$ S.D.) percent of their body weight, compared to $24.3 \pm 5.1\%$ when housed with *Hogna* (one-tailed *t*-test on the residuals of a regression of ln transformed weight gain on ln transformed carapace width, $t = -1.784$, $df = 12$, $P < 0.05$). Despite the small sample size, the results are clear: *Pardosa* alone gained almost twice the weight of *Pardosa* in the presence

of *Hogna*. This was interesting, given that the *Hogna* were hidden in refuges during the 'daylight' hours when the *Pardosa* were most active.

We have good evidence that *Hogna* has a negative influence on a fitness associated behavior, foraging, in *Pardosa*. Our field test did not reveal a strong negative effect of *Hogna* on *Pardosa*; however, *Hogna* numbers remained low in spite of repeated *Hogna* additions. It may be that *Hogna* is more prone to engage in intraspecific interactions than *Pardosa*, and so be more self-limiting. Our finding of a negative effect in the small laboratory mesocosms but not in the field coupled with the low density of *Hogna* in the field may mean that there is only a local negative effect of *Hogna* on *Pardosa*.

CONCLUSIONS

Spiders are conspicuous components of agricultural ecosystems wherever found. However, most work to date on spiders in agroecosystems has focused on the ecology of their predation on arthropod pests rather than competitive interactions. In general, the most compelling evidence for interspecific competition in spiders comes from studies undertaken in structurally simple successional habitats such as salt marshes. Can we draw any general conclusions about the likelihood and consequences of interspecific competition among spiders in agroecosystems?

Agroecosystems and littoral ecosystems, like other early successional ecosystems, are structurally simple when compared to later seral stages. This is because both are subject to regular cycles of disturbance, be it plowing in agricultural fields, or tidal or seasonal flooding as in estuarine or littoral ecosystems. Disturbance will inevitably limit the species diversity, and select for colonists which are vagile, fecund, or in other words 'weedy' (Gibson et al. 1992; Wissinger 1997). Because of the nature of the community structure in these simple ecosystems, the commonest species found there tend to occur in high densities. This, coupled with the structural simplicity of the vegetation, also increases the opportunity for interactions. The consequence is the potential for competition. Because littoral zones are ecotones between highly disturbed and less disturbed microhabitats, spider species with divergent but overlapping micro-

habitat associations may come into contact. This kind of fine-scale microhabitat segregation has been documented in lycosids (den Hollander & Lof 1972; Greenstone 1980). The zone of overlap is where we would be most likely to see competition occur, based on the studies reviewed herein. The wetland-cropland analogy is more than functional, as Luczak (1979) reports that many of what she terms 'agrobiont' spiders in Poland are naturally found in littoral ecosystems. We have likewise found that *Pardosa milvina* and *Hogna helluo* co-occur in littoral and riparian habitats as well as in the soybean agroecosystems in southwest Ohio.

The studies we reviewed, as well as ours, indicate that both exploitation and interference competition can occur between spiders. Spiller (1984) found that his species pair engaged in both, with the larger and rarer *Metepeira* dominating the smaller and more common *Cyclosa* in behavioral interactions. However, because *Cyclosa* occurred in much higher densities, it did engage in exploitation competition with *Metepeira*. This makes it unclear just which species is the competitive dominant of the pair. If we conclude that it is *Cyclosa*, by virtue of its greater densities, then the mechanism of its success is its smaller body size and apparent greater toleration of conspecifics allowing it to attain greater densities and so deplete prey. The dominant of the trio of lycosids Schaefer studied (1975) exhibited the highest densities, and engaged in interference competition with the two inferior competitors. However, in this study, as in Döbel et al. (1990), there was separation by substratum type. Competition, if observed, occurred in areas where the preferred microhabitats overlapped. This pattern of a commoner competitive dominant was not seen for the lycosids studied by Döbel et al. (1990) or Moeur (1977). In these two studies, the more aggressive competitive dominant was no more common, or in fact rarer, than the less aggressive species. In our own studies with *Hogna* and *Pardosa* we found that while *Hogna* did have a local negative effect on *Pardosa* activity, it is the rarer species in the fields (Marshall & Rypstra in press). Which is the superior competitor? *Hogna* may engage in interference competition and intraguild predation with *Pardosa*; however, we have no evidence that *Par-*

dosa exploits the prey base to the detriment of *Hogna* populations.

What is the implication of interspecific competition for biological control of arthropod pests in agroecosystems? Because spiders are generally self-limiting via agonistic interactions and cannibalism, they may have limited utility as biocontrol agents (Riechert & Lockley 1984). Between species competitive interactions could likewise limit species diversity and abundance. However, as Breene et al. (1993) note, the ability to engage in cannibalism and intraguild predation during times of low pest abundances may help maintain spider populations at some minimum in the crop fields. Spiller (1986) found that competition limited the predatory efficiency of the two species salt marsh system he worked on. He proposed that *Cyclosa* alone would better limit herbivore numbers than a combination of *Metepeira* and *Cyclosa* because the interference interactions between the two would limit *Cyclosa* densities. Luczak (1979) also proposes that spider competition should reduce prey-limitation by spider populations. However, Luczak also suggests that spider competition should be lower in littoral and agroecosystems than in ecosystems with higher spider species diversity (1979). Riechert & Lawrence (1997) on the other hand, found evidence that a multispecies spider assemblage would better reduce pest insect abundances because a group of species would occupy a wider range of niches than any single species could. In our own studies we uncovered limited evidence that *Hogna* could affect both *Pardosa* densities as well as foraging efficiency. We would predict that *Pardosa* alone would achieve greater abundances and prey population control.

Spider competition potentially occurs in agroecosystems because the community structure and physical structure of these engineered ecosystems may promote high densities of a few spider species. How important competition is in moderating the impact of spider populations on pest insect populations will depend on the spider species present in the fields.

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THE IMPLICATIONS OF INTRAGUILD PREDATION FOR THE ROLE OF SPIDERS IN BIOLOGICAL CONTROL

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ABSTRACT. Evidence is growing that spiders can be effective biological control agents, particularly assemblages of several species. Other evidence finds that spiders prey on each other and other generalist predators, and as such are of limited value in biological control. Such predatory interactions between species which use similar resources have been dubbed intraguild predation (IGP) due to their potential to modify competition as well as cause direct mortality. IGP interactions can have unexpected effects at other trophic levels, and sometimes result in enhancement of a pest population. In this paper I review the evidence for intraguild predation interactions involving spiders in natural systems, and other generalist predators in agroecosystems. To date not much research has examined whether such interactions influence spider biological control potential. Some suggestions as to how we might begin to address these issues are presented.

Given their generalist arthropod diet and abundance in most terrestrial habitats, spiders likely inflict substantial mortality on insect populations. While the mechanisms by which spiders limit insect prey populations have been debated (Riechert & Lockley 1984; Wise 1993), it is generally agreed that they are important in reducing insect numbers, and as such are of potential value in biological control (Riechert & Lockley 1984; Nyffler & Benz 1987; Young & Edwards 1990; Wise 1993). Several studies have shown that assemblages of many predator species may be more effective at controlling agricultural pests than single species augmentation (Chiverton 1986; Riechert & Bishop 1990; Clark et al. 1994; Provencher & Riechert 1994; Chang 1996; Riechert & Lawrence 1997). On the other hand, different species of predators and/or parasitoids may compete with or prey on each other, potentially reducing their biological control potential (Force 1974; Ehler & Hall 1982; Spiller 1986; Briggs 1993; Rosenheim et al. 1995; Chang 1996; Ferguson & Stiling 1996; Kester & Jackson 1996; Cisneros & Rosenheim 1997; Rosenheim 1998).

The nature of the diet of spiders suggests that they can prey on each other and other arthropod predators (Polis 1981; Jackson 1992; Wise 1993), as well as overlap in prey taxa consumed, thus potentially competing for resources. Diet overlap is one distinguishing feature of a guild, a group of sympatric taxa

that use similar resources (Root 1967; Polis et al. 1989; Simberloff & Dayan 1991). Predatory interactions among members of the same guild are termed intraguild predation (IGP). This is distinguished from predation as traditionally defined because, by eating a guild member, an individual not only directly gains energy and nutrients, but also reduces potential competition for food (Polis et al. 1989; Polis & Holt 1992). Intraguild predation and cannibalism (killing and eating a member of the same species), may have profound effects on community structure (Polis 1981, 1988; Polis et al. 1989; Polis & Holt 1992). Given their ubiquity in terrestrial ecosystems, spiders are model organisms to investigate the occurrence and consequences of IGP.

IGP: predation among potential competitors.—Intraguild predation and cannibalism have been shown to directly limit predator populations (Polis & McCormick 1986, 1987; Spiller & Schoener 1988; Wissinger 1989; Leonardsson 1991; Finke 1994; Wagner & Wise 1996; Wissinger et al. 1996). Since unsuccessful predation attempts represent extreme forms of interference competition (Polis et al. 1989; Elgar & Crespi 1992), IGP can also lead to behavioral adaptations to reduce mortality and conflict, resulting in habitat and diet shifts by IG prey (Fox 1975; Turner & Polis 1979; Doncaster 1992; Sih 1982; Ebenman & Persson 1988; Foster et al. 1988; Polis et al. 1989; Polis 1993; Dong & Polis 1992;

Holt & Polis 1997). These changes in foraging and habitat distribution may in turn have effects at other trophic levels (Polis 1984; Wilbur 1988).

The traditional view of feeding relationships has been to assign species in a community to a "trophic-level", such as secondary consumer (predator), primary consumer (herbivore), primary producer (plant), and so forth, with each level feeding on the former (Krohne 1998). Thus, in classic biological control, insect herbivore populations are reduced by addition of predators, and this in turn reduces damage to crop plants (van den Bosch et al. 1982). In reality, however, animals may feed from a variety of trophic levels, especially generalist predators, which take prey of whatever size they can handle (Polis 1988; Polis et al. 1989; Spence & Carcamo 1991; Dong & Polis 1992; Finke 1994). If these prey include younger conspecifics or other predators, then control of the herbivore population is not guaranteed. Various studies suggest that direct effects of one predator on another can indirectly affect a shared prey species by releasing it from intense predation or competition (Press et al. 1974; Pacala & Roughgarden 1984; Hurd & Eisenburg 1990; Polis & Holt 1992; Rosenheim et al. 1993; Wissinger & McGrady 1993; Wootton 1993; Cisneros & Rosenheim 1997; Fagan & Hurd 1994). If shared prey are herbivores then the indirect effects could cascade to plants, influencing primary productivity, an issue of agricultural relevance. The purpose of this paper is to review the theory and empirical evidence relevant to the implications of IGP for the potential role of spiders in biological control of herbivorous pests in agriculture.

IGP between spiders and other generalist predators.—Several studies of IGP in natural communities have uncovered direct and indirect interactions involving spiders. Polis & McCormick (1986, 1987) investigated a desert community of arachnids including spiders, solpugids and scorpions, all generalist predators that use similar prey and prey on each other. Scorpions were continually removed from experimental plots, but not from control plots, and the relative abundances of the spiders and solpugids were tracked over time. At the end of the experiment (29 months), significantly more spiders occurred in the scorpion removal plots than in the control plots.

Two alternative hypotheses could explain these results: removal of the scorpions could have resulted in competitive release by the spiders in experimental plots, or IGP (by scorpions) in the control plots may have reduced spider population size. There was no evidence of competitive release in that there were no differences between the experimental and control plots in insect prey abundance or spider reproduction. Release from scorpion predation was the most likely cause of the increased numbers of spiders.

Two independent studies on *Anolis* lizards examined evidence for intraguild predation on spiders cascading to populations of shared insect prey. Pacala & Roughgarden (1984) manipulated anole densities in a Caribbean forest and found a direct effect of lizards on forest floor arthropods, their primary prey, and an indirect effect on flying insects, the prey of orb-weaving spiders. Since anoles also prey on orb-weavers, the increase in flying insects on the high density lizard plots was thought to be due to intraguild predation by the lizards on the spiders. On Bahamian islands Spiller & Schoener (1990) also found a direct effect of lizards on spiders, but no indirect effect on flying insects. They did, however, observe that more spiders were feeding on lizard removal plots than on plots where they co-existed with lizards. The authors hypothesized that interference competition or predation by lizards may displace spiders from prime web-sites, resulting in a reduction in prey capture for the spiders.

Although the generalist diet of most spider species suggests that exploitative competition for food should be important (Marshall & Rypstra, this volume), experimental tests have found little evidence (Schaefer 1978; Wise 1981; Horton & Wise 1983; Riechert & Cady 1983; see Spiller 1984 a, b for an exception). In spider removal experiments to test for exploitative competition among four genera of web-building spiders, Riechert & Cady (1983) not only found no competitive release, but on some of their removal plots they observed a negative effect of spider removals on the species remaining. They hypothesized that this may have been due to the fact that by removing the other species of spiders, they may have been removing potential prey.

Hodge & Marshall (1996) tested Riechert & Cady's hypothesis that intraguild predation

masked competitive release in their system of web-building spiders on rock outcrops in Tennessee. After 12 weeks of removing each of three species from experimental plots we found that one of the species, *Hypochilus thorelli* (Araneae, Hypochilidae) had lower body condition indices (indicating lower fecundity, Jakob et al. 1996) on spider removal plots as compared to control plots. This species was the major intraguild predator in the system, with spiders comprising over 40% of its diet (Riechert & Cady 1983; Hodge & Marshall 1996). These results support Riechert & Cady's interpretation of the lack of competitive release in their study. Another species, *Achaearenea tepidariorum* (Araneae, Theridiidae) exhibited greater spiderling populations on rock outcrops from which the other two species had been removed as compared to control plots, suggesting that the manipulation removed predators (Hodge & Marshall 1996). The fact that this study found IGP-related effects was striking given that the removals occurred over a relatively short time frame.

Hurd & Eisenberg (1990) examined how interactions between praying mantises (*Tenodera sinensis*) and wolf spiders (*Lycosa (Rabidosia) rabida*) affected overall arthropod numbers in a temperate early successional field habitat. They established four treatments, each of which enclosed a cubic meter of old-field vegetation in screen cages: mantids alone, wolf spiders alone, mantids and wolf spiders, and a control with neither predator added, and then sampled the number and biomass of other arthropods after 10 days. The 'mantids alone' enclosures had lower arthropod biomass than any of the other treatments. Examining the arthropods on a taxa-by-taxa basis revealed that in the 'wolf spiders alone' treatments there was a significant increase in the density of crickets as compared to the other treatments. The explanation for this counter-intuitive result illustrates the complexity of direct and indirect effects that can result from IGP interactions. The authors concluded that interactions between wolf-spiders (as evidenced by some cannibalism) decreased their effectiveness as predators on crickets, and that in mantid/lycosid enclosures this effect was ameliorated because of mantid impact on spider numbers (an indirect effect of mantids on crickets). The presence of lycosids on the

ground caused the crickets to move upward on vegetation (a direct effect of spiders on crickets); but when present with both mantids and lycosids, crickets were captured by mantids hunting in the vegetation. Finally, lycosids may have consumed other cricket predators (other spiders; an indirect effect of spiders on crickets); this was supported by the finding that there were significantly fewer heterospecific spiders in the lycosid enclosures. These results should be of interest to biological control because mantids are often augmented, at least in small scale crop systems. On the other hand one may question the reality of this experiment since many predators were packed into small enclosures, whereas normally they could flee from one another.

Enclosure effects were not a factor in the open-plot studies performed by Moran & Hurd (1994) in the same system. They added first instar mantids to 2 m × 2 m plots separated by 2 m wide barriers of black plastic sheeting which had a band of insect trapping compound painted down the middle to intercept arthropods leaving the plots. By comparing arthropods captured around mantid addition plots to those captured around control (no mantids) plots, they discovered a behavioral response by spiders to the presence of elevated mantid densities. Spiders dispersed from plots in which mantids were augmented. Smaller spiders (< 8 mm) are prey of the mantids whereas larger spiders (primarily wolf spiders) prey on the mantid nymphs and smaller spiders. Larger wolf spiders may have departed mantid addition plots because smaller spiders had dispersed. In this case the threat of IGP caused smaller spiders to leave, and scarcity of this IG prey caused the larger spiders to leave. Addition of supplemental food (*Drosophila*) reduced the tendency for spiders to emigrate from mantid augmented plots (Moran & Hurd 1997). This in turn increased IGP by spiders on mantids, as their numbers tended to decline in the food supplemented plots. As the authors point out, alternative prey does not always benefit generalist predators if they can prey on one another.

These authors extended their investigation to include the possibility of trophic cascades (Moran et al. 1996; Moran & Hurd 1998). Of interest was how a diverse plant community would respond in the context of an assemblage of many predator and herbivore species.

In these experiments, control plots had no mantids, and experimental plots had natural densities of mantids. Cursorial spiders emigrated from mantid plots throughout the course of the study (2 months) (Moran et al. 1996). Early emigration was probably due to the threat of IGP by mantids, whereas later emigration may have been a result of competition for prey, since mantid numbers at this point in time were too low to cause predator avoidance. Herbivore biomass was significantly lower and plant biomass was 30% higher in the mantid addition plots by the end of the experiment. Mantids therefore caused a trophic cascade that extended to plants.

These studies demonstrate that, contrary to theoretical predictions that interactions between trophic levels in complex communities will be diffuse and buffer the intensity of responses of any given species to another (Strong 1992), a single predator in a speciose natural assemblage can indeed initiate a trophic cascade. Perhaps this bodes well for potential predator influences on primary production in less speciose agroecosystems: that is, despite the potential for IGP, strong interactions can cascade through trophic levels in such a way as to benefit crops. On the other hand, these strong interactions could be such that IGP interactions disrupt rather than enhance the control of herbivore populations (Rosenheim et al. 1993; Rosenheim 1998).

IGP in agroecosystems.—The fact that the self-limiting nature of spiders (via interference, territoriality or araneophagy) can decrease their potential as biological control agents has been recognized (Reichert & Lockley 1984; Wise 1993), but rarely quantified. The bulk of my review will therefore cover experimental studies involving IGP among arthropod generalist predators other than spiders, since they have as yet not been well studied.

Rosenheim et al. (1993) examined interactions between three species of predatory hemiptera (*Geocoris* spp., *Nabis* spp., and *Zelus renardii*) and green lacewing larvae (*Chrysoperla carnea* (Neuroptera)), all of which eat aphid pests (*Aphis gossypii*) of cotton. To determine whether hemipteran predators exert mortality on lacewings, they caged cotton plants with aphids alone (control), and aphids with various combinations of the hemipterans. Lacewing survival was significantly reduced

in the presence of bugs. To isolate the influences of predation cotton plants were caged with a variety of combinations of predators: each hemipteran species alone or in combination with lacewing larvae (with appropriate controls). Lacewing survival was significantly lower in the *Z. renardii* and *Nabis* spp. treatments. Comparing aphid population growth among the single-predator species treatments, only in those cages with lacewing larvae alone was there a significant impact on aphids, suggesting that of all of these predator species, lacewings are the most effective at aphid control. Given these results, it is not surprising that cages with lacewing larvae and *Z. renardii* or *Nabis* spp. exhibited a non-additive effect on aphid population control. Not only were the effects non-additive, but aphid populations actually increased in these treatments. Therefore, predator interference generated a trophic cascade, increasing the abundance of herbivores.

They also examined the effect that nymphal hemipterans can have on lacewing eggs. The presence of hemipterans reduced the proportion of lacewing eggs surviving to larval stages. Cisneros & Rosenheim (1997) examined the effect of predation by *Z. renardii* of different age-size classes on control of cotton aphid populations by lacewing larvae. Survival of lacewing larvae was significantly lower in the presence of larger, older *Zelus*, and this produced a significant disruption of lacewing control of aphid populations. Observations of freely foraging bugs in the field showed an ontogenetic shift in foraging height and foraging behavior resulting in higher encounter rates between *Zelus* adults and other predators (Cisneros & Rosenheim 1998).

Another study of aphidophagous predators examined interactions between generalists and specialists and evaluated predator mobility as a potential factor influencing vulnerability to IGP (Lucas et al. 1998). The predators were lacewings (*Chrysoperla rufilabris*), spotted lady beetles (*Coleomegilla maculata*), both generalists, and larvae of the gall midge (*Apidoletes aphidimyza*), a specialist on the shared prey, potato aphids (*Macrosiphum euphorbiae*). The lacewing and lady beetles are very active foragers as larvae and adults, whereas gall midge larvae are slow-moving predators.

IGP interactions between all three predators

were investigated in the absence of aphid prey. Various combinations of predators at different developmental stages (egg-adult) yielded 37 different test combinations. Symmetric IGP occurred between lacewings and lady beetles; that is, larger developmental stages of one predator fed on smaller developmental stages of the other. A few exceptions were explained by behavioral and morphological differences between the predators. Third instar lacewings were able to prey on larger fourth instar lady beetles as well as adult beetles. It may be that a more aggressive hunting style and effective grasping mouthparts of lacewings allow them to defy the general trend that the larger predator wins (Lucas et al. 1998). Interactions between both lacewings and lady beetles with gall midges were asymmetric: gall midges were almost never IG predators. This confirmed the authors' prediction that more mobile predators have an advantage over slow moving predators.

In the presence of shared or extraguild prey (potato aphids) IGP was lower in several of the predator/life-stage combinations. Some of the IGP interactions persisted though, except when extraguild prey densities were very high. Based on the outcomes of IGP interactions between their different predators at various levels of extraguild prey, Lucas et al. (1998) developed some general predictions as to the effect of extraguild prey and predator characteristics on the direction and outcome of IGP interactions. In cases where both predators forage randomly, IGP will decrease steadily with increasing extraguild prey. Random search will, in this case, bring predators into contact with extraguild prey more often. When IGP interactions are risky for both predators, IGP should decrease exponentially as extraguild prey increases in density. Abundance of alternative prey has similarly been observed to influence the tendency towards cannibalism in many animals (Elgar & Crespi 1992). In some cases IGP may remain constant despite increasing extraguild prey, especially if IG prey are vulnerable, sessile and/or aggregated. Finally, IGP may remain high at low extraguild prey densities, and only decline at very high extraguild prey densities. When extraguild prey are at low density, IG predators may benefit from removing potential competitors, whereas at high prey density this benefit disappears. Overall, the theme that

unifies all of these predictions, and all of the experimental studies presented above, is that a detailed understanding of the ontogeny, behavior and ecology of predators and prey is required to understand the role that IGP plays in the dynamics of complex communities, including agroecosystems.

IGP & spiders in agroecosystems.— Though some research has been conducted evaluating the effectiveness of spiders as bio-control agents in agroecosystems (Riechert & Bishop 1990; Clark et al. 1994; Provencher & Riechert 1994; Carter & Rypstra 1995; Riechert & Lawrence 1997), there has been scant research on their potential interactions with other predators. Fagan et al. (1998) discovered an unpredicted interaction between IGP, pesticide application and biological control. They set out to examine the compatibility of insecticide-based and natural enemy-based pest control methods in tropical rice. Using open-top cages (to ameliorate enclosure effects) they established four treatments: insecticide added, wolf spiders added, both insecticide and wolf spiders added, nothing added. As would be predicted, rice pests were lower in the insecticide and wolf spider treatments, and each reduced pest densities to similar levels. The combination of insecticide and wolf spider addition, however, resulted in an increase in pests such that these enclosures were indistinguishable from the controls. They attribute these results to the additive impact of spiders and insecticide on predatory hemipterans (mesoveliids) which are also important biological control agents of rice pests. The combination spider-insecticide treatment lowered the densities of these alternative predators below the threshold of effective biological control. This study has important implications for integrated pest management, and further illustrates the importance of a clear understanding of the role of IGP in agricultural systems.

Given the general lack of experimental studies, what evidence (beyond Fagan et al. 1998) do we have that IGP involving spiders might be important in agroecosystems? Several studies have documented that spiders do engage in IGP interactions with other generalist predators, and many of these observations come from crop systems (Table 1). These data were gleaned from tables in primary research papers and from several reviews of spider diets by Nyffeler and col-

Table 1.—A survey of the literature containing field observations of the spectrum of prey captured by a variety of spider species focusing on taxa that are potentially intraguild prey. The percent of the total observed diet for the majority of species in the list is obtained from a total number of observed prey exceeding 50.

IG predator	IG prey taxon	% of diet	Habitat	Source
Araneidae:				
<i>Argiope bruennichi</i>	Araneae	3.3	Grassland	Nyffeler 1982
Linyphiidae:				
<i>Oedothorax insecticeps</i>	Araneae	16.3	Rice	Kiritani et al. 1972
Theridiidae:				
<i>Latrodectus mactans</i>	<i>Solenopsis in-victa</i>	75.3	Cotton	Nyffeler et al. 1988
<i>Achaeareanea tepidario-rum</i>	Araneae	22	Rock outcrop	Hodge & Marshall 1996
Lycosidae:				
<i>Paradosa</i> spp.	Araneae	6.8	Winter Wheat	Nyffeler & Benz 1988
<i>Paradosa ramulosa</i>	Araneae	19.6	Alfalfa	Yeargan 1975
<i>Lycosa pseudoannulata</i>	Araneae	8.9	Rice	Kiritani et al. 1972
<i>Lycosa antelucana</i>	Lycosidae	4	Cotton	Hayes & Lockley 1990
<i>Lycosa antelucana</i>	Staphylinidae	6.7	Cotton	Hayes & Lockley 1990
<i>Lycosa antelucana</i>	Carabidae	10.9	Cotton	Hayes & Lockley 1990
unspecified	Araneae	19.2	Peanuts	Agnew & Smith 1989
<i>Pardosa lugubris</i>	Araneae	24	Forest	Edgar 1969
<i>Pardosa lugubris</i>	Araneae	34	Forest	Hallander 1970
<i>Pardosa amentata</i>	Araneae	11	?	Edgar 1970
<i>Pardosa pullata</i>	Araneae	38	Meadow	Hallander 1970
<i>Pardosa purbeckensis</i>	Araneae	23	Salt Meadow	Nyffeler & Benz 1988
<i>Pardosa ramulosa</i>	Araneae	20	Alfalfa	Yeargan 1975
<i>Pardosa hokkaido</i>	Araneae	12	Forest	Suwa 1986
<i>Pirata piraticus</i>	Araneae	22	Salt Meadow	Schaefer 1974
<i>Pirata piraticus</i>	Araneae	28	River Bank	Gettmann 1977, 1978
<i>Pardosa agrestis</i>	Araneae	16	?	Nyffeler 1982
<i>Lycosa osceola</i>	Araneae	27.5	Florida scrub	Hodge, unpublished
<i>Lycosa pseudoceratiola</i>	Araneae	9	Florida scrub	Hodge, unpublished
Oxyopidae:				
<i>Oxyopes salticus</i>	Araneae	15.9	Cotton	Nyffeler et al. 1992
<i>Oxyopes salticus</i>	Araneae	14.1	Cotton	Nyffeler et al. 1987a
<i>Oxyopes salticus</i>	Araneae	9	Cotton	Nyffeler & Sterling 1994
<i>Peucetia viridans</i>	Araneae	40	Cotton	Nyffeler et al. 1987b
<i>Peucetia viridans</i>	Hemiptera	8	Cotton	Nyffeler et al. 1987b
<i>Peucetia viridans</i>	Neuroptera	8	Cotton	Nyffeler et al. 1987b
<i>Peucetia viridans</i>	Araneae	16	Croton	Nyffeler et al. 1987b
<i>Peucetia viridans</i>	Araneae	13.3	Peanuts	Agnew & Smith 1989
<i>Peucetia viridans</i>	Araneae	7	shrubs	Turner 1979
various	Araneae	15	?	Nentwig 1986
Thomisidae:				
<i>Xysticus</i> spp.	Araneae	6.4	Meadow: Plants	Nyffeler 1982
<i>Xysticus</i> spp.	Araneae	26	Meadow: Soil Sur-face	Nyffeler 1982
<i>Misumenops</i> spp.	Araneae	16.7	Peanuts	Agnew & Smith 1989

Table 1.—Continued

IG predator	IG prey taxon	% of diet	Habitat	Source
Salticidae:				
<i>Phidippus audax</i>	Araneae	22.2	Wild Plants & Cotton	Dean et al. 1987; Nyffeler et al. 1994
<i>Phidippus audax</i>	Araneae	15.5	?	Young 1989
<i>Phidippus johnsoni</i>		27	?	Jackson 1977
various	Araneae	20	?	Nentwig 1986
Amaurobiidae				
<i>Coras montanus</i>	Araneae	24	Rock outcrop	Hodge & Marshall 1996
Hypochilidae				
<i>Hypochilus thorelli</i>	Araneae	46	Rock outcrop	Hodge & Marshall 1996
Pisauridae				
<i>Pisaura mirabilis</i>	Araneae	18	?	Nitzsche 1981
Pholcidae				
<i>Pholcus phalangiodes</i>	Araneae	6	Cellars	Nentwig 1983
Scytodidae				
<i>Scytodes longipes</i>	Araneae	17.4	outside buildings	Nentwig 1985
Unspecified Araneae	Hemiptera	14.5	Peanuts	Agnew & Smith 1989
	Araneae	17.3	Peanuts	Agnew & Smith 1989

leagues. Higher levels of IGP might have been reported in some cases if more specific taxonomic categories were used, for example, breaking insect orders into families which often exhibit characteristic feeding habits (e.g., Carabidae rather than Coleoptera). Even so, it is not uncommon to find spider diets consisting of almost one-fifth IG prey (mean for Table 1 = $18.3\% \pm 12.7\%$).

It is hard to form any general conclusions based on the data in Table 1 since the list is not comprehensive, and the methodology and intensity of data collection vary among studies. The most striking feature, however, is the number of studies involving lycosids and oxypids in agricultural systems, and the sometimes high percentage of IG prey reported from these spiders (e.g., 40% Araneae in the diet of *Oxyopes salticus*). It may be that cursorial spiders dominate as IG predators due to their active hunting style (Lucas et al. 1998; Cisneros & Rosenheim 1998). It would be quite informative to have greater taxonomic resolution to the IG prey reported, to see if they are represented disproportionately by less mobile predators. This type of resolution would also suggest the types of direct and in-

direct effects that might cascade to herbivores and crops.

CONCLUSIONS

How can we determine the implications of IGP for the role of spiders in agroecosystems? How does one begin to identify which of a suite of predators present in a particular crop have the potential for IGP interactions? Classification systems exist for spider guilds (Uetz et al., this volume), predator and herbivore guilds in crops (Breene et al. 1993) and structural zones in crop plants which may support distinct suites of predator and prey species (e.g., LeSar & Unzicker 1978). Using these as a starting point, one can begin to define potential predator-predator and predator-herbivore interactions in which IGP may be of consequence. Quantification of the potential for IGP and/or competition should be achieved by careful study of the relative densities, habitat use, activity period and space, and diet. From these measures one can calculate indices of the opportunity for predation (IOP) and the opportunity for competition (IOC), as derived by Wissinger (1992) from pre-existing indices of resource overlap (Hurlbert 1978). Wissinger

ger's indices allow for comparisons of the relative strengths of predation, cannibalism, and resource competition between and within species by quantifying these interactions in the field and laboratory (Wissinger 1992). In a sense, they simply involve collecting the relevant natural history information about each species, and quantifying this information to make specific predictions of the relative importance of cannibalism, IGP and intra- or interspecific competition. This allows the design of more rigorous and meaningful field experiments (Wissinger 1992).

Future field experiments should heed lessons from the past regarding the use of enclosures and the duration of experiments. Stocking closed cages with predators may not reveal information relevant to the real world; and responses in the short term may lead to very different conclusions than might be reached from experiments of duration more similar to the actual seasonality of the particular system (Wise 1993; Moran & Hurd 1994, 1998), and should be repeated across years to detect the effects of temporal variability (Polis et al. 1998).

Despite the recent revival of interest in food web interactions, ("top-down" versus "bottom-up" effects) and the complex nature of feeding relationships (Strong 1992; Polis 1994; Polis & Strong 1996; Polis & Wine-miller, 1996; Holt & Polis 1997), the scenario still generally used for biocontrol is that of a 3-tiered system in which herbivores eat plants, and in turn are eaten by predators. As the studies reviewed in this paper demonstrate, animals do not recognize these artificial trophic boundaries, and often feed from several trophic levels. This can generate a complex array of direct and indirect effects which can have important and unexpected consequences for the effectiveness of generalist predators as biological control agents. The paucity of experimental research on the potential web of IGP interactions involving spiders is surprising since they are widely recognized as model organisms for the types of manipulative field studies used to investigate these interactions (Polis 1993; Wise 1993). Other generalist predators studied to date (hemiptera, lacewings, beetles) are similar in nature to spiders in that they include animals with a both sit and wait and active foraging hunting styles, and also involve animals with distinct size

classes, generating possibilities for both cannibalism and intraguild predation between different life stages of different predator species. Given the variety of crop systems, management practices (e.g., tillage versus no-tillage), and diverse predator and prey assemblages, agricultural systems provide models for investigating the role of IGP from both pure and applied perspectives.

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SPIDERS IN DECOMPOSITION FOOD WEBS OF AGROECOSYSTEMS: THEORY AND EVIDENCE

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ABSTRACT. The involvement of spiders in decomposition food webs has the potential to affect agricultural productivity through two quite different types of interactions: (1) cascading, top-down effects of spider predation on rates of nutrient mineralization—spider-initiated trophic cascades in the detrital food web that could alter rates of decomposition and release of nutrients to plants; and (2) a bottom-up linkage, through spiders, between decomposition and grazing food webs—energy from the detrital web contributing to elevated spider densities, which in turn might reduce pests and enhance net primary production. Scant experimental evidence exists to refute or support either hypothesis. The first set of interactions is most likely to be of significance in no-till and conservation tillage farming. In theory, spiders have the potential to enhance productivity by increasing rates of mineralization, but theory also predicts that spiders, by preying on important detritivores and fungivores, depress rates of litter decomposition. Field experiments by Kajak and her colleagues have uncovered such negative effects of spiders in mown pastures. Although this negative effect could reduce plant growth, the expected time lags in most types of crops suggest that the overall impact of spiders on plant production will be determined more by the interactions comprising the second hypothesis. However, the later hypothesis, that bottom-up control processes in the decomposition web affect crop productivity via energy subsidies to spiders and other generalist predators in the grazing web, remains conjecture without clear experimental confirmation. This hypothesis should be tested in agroecosystems in which detritus-based food webs can feasibly be manipulated.

A major goal of agriculture is to maximize net primary production, which is the ultimate source of energy for both grazing and decomposition food webs. Biocontrol practitioners have focused on the grazing web because agricultural pests and humans compete directly for the living products of photosynthesis. Thus, research on the roles of spiders in agroecosystems has focused primarily on the extent to which these predators suppress densities of grazing herbivores. Spiders also belong to decomposition food webs of agroecosystems, yet arachnid connections to such webs have stressed acarine cousins; and spiders have been largely ignored. Is this neglect justified, or might knowledge of how spiders function in decomposition food webs be utilized to increase agricultural yields?

Two quite different sets of interactions between spiders and the detritus-based food web are potentially relevant. The first set involves

cascading, top-down effects of spider predation on rates of nutrient mineralization—spider-initiated trophic cascades in the detrital food web that could affect rates of decomposition and release of nutrients to plants. The second set of interactions relies on a linkage, through spiders, between decomposition and grazing food webs—energy from the detrital web contributing to elevated spider densities, which in turn might cause lower pest numbers and enhanced net primary production. Here we examine the evidence that these two different sets of interactions affect, or have the potential to influence, agricultural productivity.

TOP-DOWN TROPHIC CASCADES AND RATES OF DECOMPOSITION

Theory.—Decomposition food webs are often categorized as “donor-controlled” systems (Pimm 1982) because the rate at which detritus is consumed does not immediately influence the rate of supply of this energy to the system, but the amount of detrital input can influence densities of detritivores and their

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predators. Viewing detrital food webs as primarily donor-controlled leads to the conclusion that bottom-up control processes predominate in such webs, i.e., that most linkages of indirect effects are responses to changes in rates of input at the base of the food web. This view is an over-simplification for at least two reasons. First, the rate at which the primary decomposers—the bacteria and fungi, collectively known as the microflora—decompose detritus depends on their population growth rates, which in turn are potentially influenced by their natural enemies (Swift et al. 1979). The second oversimplification is that, ultimately, decomposition processes affect net primary production by altering rates of mineralization, i.e., the rates at which nutrients locked in detritus become available to autotrophs. As a consequence, spiders that feed on detritivores have the potential to influence indirectly the growth of autotrophs by generating trophic cascades in the decomposition food web, thus affecting rates at which nitrogen and other nutrients required by plants enter the nutrient pool.

Such linked indirect effects most likely occur in those agroecosystems in which a substantial fraction of litter decomposition occurs on the soil surface, and in which the major consumers of detritus and the microflora are preyed upon by spiders. Ploughing disrupts the litter layer and distributes organic matter throughout the soil; thus, cultivation encourages below-ground, bacterial-based decomposition food webs (Hendrix et al. 1986). The role of spiders in such webs is likely insignificant. Under no-till and conservation tillage conditions, however, litter accumulates above ground, fungi are a major component of the microflora, and microarthropods, primarily mites and Collembola (springtails), are major detritivores/fungivores (Hendrix et al. 1986; Stinner & House 1990; Robertson et al. 1994). Spiders readily consume Collembola, which constitute a substantial portion of the diet of many species (Hallander 1970; Schaefer 1975; Yeargan 1975; Wingerden 1975, 1978; Greenstone 1980, 1983; Nentwig 1987; Döbel & Denno 1994; Nyffeler et al. 1994). Hence spiders are most likely to exert a trophic cascade affecting mineralization in no-till annual crops; and in orchards, pastures and other perennial crops.

Spiders have the potential to generate either

positive or negative impacts on rates of mineralization, even if one ignores interactions between spiders and other predators. The simplest abstract food chain in a spider-influenced system would consist of three effective trophic levels: detritus, Collembola (realizing that other detritivores play roles similar to Collembola, but Collembola appear to be ubiquitous and abundant), and spiders. The indirect effects of spiders in such a food chain would be to enhance the standing crop of detritus, i.e., to retard the rate of litter decomposition (Fig. 1A). This model, however, is greatly oversimplified. Fungi play a critical role in decomposing plant litter; and although Collembola consume plant material, many Collembola species are primarily fungivorous (Peterson 1971; Chen et al. 1996). Thus a four-level food chain model is more realistic (Fig. 1B). In grazing food chains of four trophic levels, predators can induce a trophic cascade that negatively impacts the base trophic level—the primary producers. Reasoning by analogy, one might predict that an increase in spider density should lead to a decrease in the amount of detritus, i.e., an increase in decomposition rate, by relieving predation pressure on fungi (Fig. 1B). However, does an increase in fungal biomass always lead to increased rates of mineralization? Not necessarily, because nutrients can become immobilized in senescent fungal hyphae. Thus, Collembola at intermediate densities can enhance rates of mineralization by consuming senescent fungal hyphae (Parkinson et al. 1977; van der Drift & Jansen 1977; Warnock et al. 1982; Finlay 1985; Verhoef & de Goede 1985; Visser 1985). Collembola also enhance decomposition by more indirect pathways, i.e., by comminuting the litter (Anderson et al. 1984). Therefore, depression of Collembola populations by spiders could negatively impact rates of litter decomposition and mineralization (Fig. 1C).

It is clear that the potential relationship between spider densities and mineralization rates is complicated because links between Collembola density and rates of litter decomposition are complex. Field experiments in which spider densities are reduced is the most direct way to determine which of the competing hypotheses about possible spider-induced trophic cascades is correct.

Evidence.—Kajak and her colleagues have

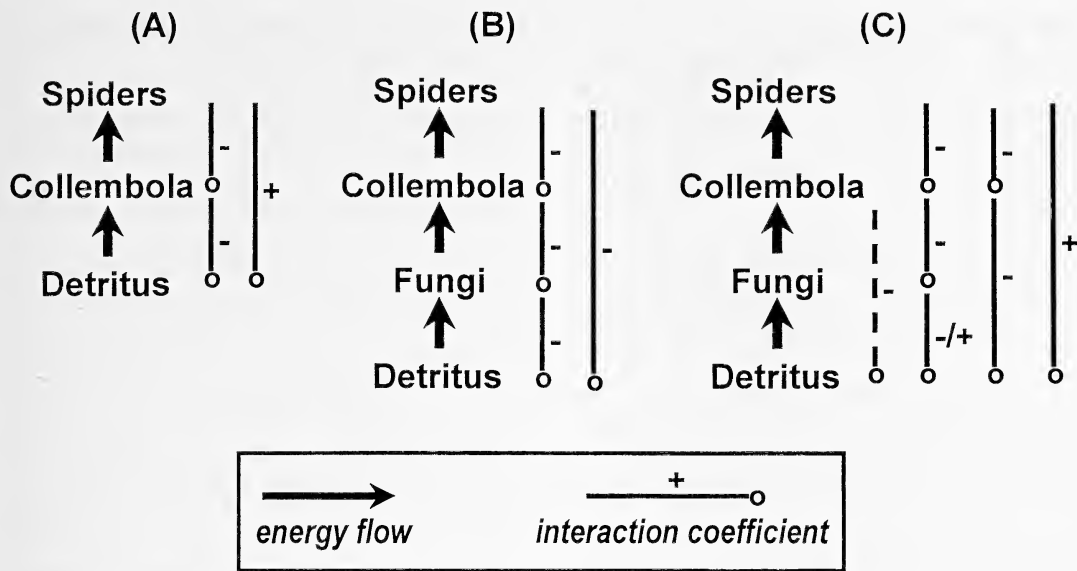


Figure 1.—Three different hypothesized sets of trophic cascades in which predation by spiders on Collembola might either enhance or retard rates of litter decomposition. (A) A 3-level food chain in which indirect effects of predation by spiders retard decomposition, indicated by a net + influence of spiders on the amount of detritus $[(-) \times (-) = (+)]$. (B) A simple food chain of 4 trophic levels in which spider predation enhances litter decomposition, i.e., decreases litter amount $[(-) \times (-) \times (-) = (-)]$. (C) A more realistic food chain model, in which indirect effects of spider predation are predicted to retard decomposition rate. This model incorporates the positive non-trophic effects of Collembola feeding, such as litter comminution, on rates of fungal growth; and the fact that the relationship between fungal density and rates of fungal breakdown is non-linear.

studied the impact of spiders and other generalist arthropod predators—primarily carabid beetles—on rates of litter decomposition in mown meadows (Kajak & Jakubczyk 1975, 1976 1977; Kajak & Kaczmarek 1988; Kajak et al. 1991; Kajak 1997). Their basic approach has been to exclude epigeic macrofauna from small field cages, and then compare trapping rates of predators; densities of Collembola, other fungivores/detritivores, and the microflora; and rates of litter decomposition, with corresponding rates and densities in partially open cages or open areas.

In some of their studies not all differences were statistically significant, and some variation occurred between experiments conducted in different meadows and different years. Nevertheless, a clear pattern emerges. Excluding macrofaunal predators, of which spiders comprise a substantial fraction, frequently causes an increase in Collembola and other mesofauna and an increase in rates of litter decomposition. Thus ambient densities of spiders and other macrofaunal predators inhibit rates of decomposition in grasslands.

These studies were conducted in a managed system in which the diversity of vegetation, fauna and microflora probably is more similar to that of more natural ecosystems than to highly disturbed crop systems. To date available evidence supports the hypothesis that spiders inhibit rates of decomposition and mineralization (Fig. 1C); and evidence does not support the alternative hypothesis, that spiders increase crop productivity through trophic cascades within the decomposition food web. Clearly more experiments of the type conducted by Kajak and her colleagues are needed in a variety of agroecosystems.

DETRITAL SUBSIDY OF THE GRAZING FOOD WEB

Theory.—Spiders, because they prey upon both detritivores/fungivores and herbivores, simultaneously belong to decomposition and grazing food webs. The connection of spiders to both webs opens the possibility that increased input of detritus to the agroecosystem could enhance detritivorous and fungivorous prey of spiders, leading to elevated spider

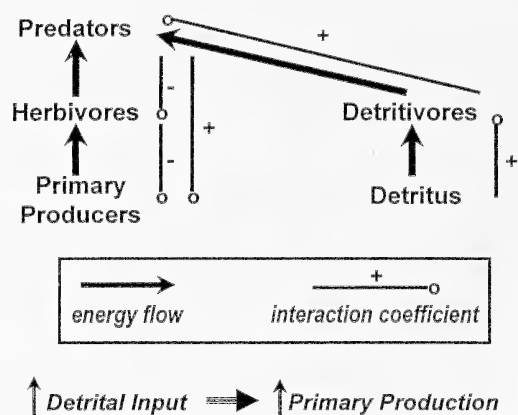


Figure 2.—If decomposition and grazing food webs are linked by common top predators, it is possible that increased input of detritus could elevate the biomass of primary producers through a complex linkage of trophic interactions (i.e. apparent competition between detritivores and grazing herbivores). Because in this model the predators are feeding on more than one trophic level and there is an external input of energy to the grazing food chain, this type of effect on the grazing food web has been termed an *allochthonous energy subsidy via multichannel omnivory* (Polis 1994; Polis & Strong 1996).

densities which in turn would increase pressure on herbivores, thereby enhancing rates of net primary production. In this way increased input of detritus could, in principle, make spiders more effective biocontrol agents by introducing an energy subsidy to the grazing food web. This complex series of indirect effects involving bottom-up control processes in one food web and top-down processes in another is an example of an *allochthonous energy subsidy via multichannel omnivory* (Polis 1994; Polis & Strong 1996; Fig 2). An example from non-agricultural systems is the input of detrital energy from the marine environment that leads to elevated densities of spiders and other predators in coastal areas, with subsequent declines in herbivores and reduced plant damage (Polis & Hurd 1996). Food-web interconnections in tropical rice fields, in which detritus is both allo- and autochthonous, constitute a probable example from agricultural systems. Settle et al. (1996) argue that abundant populations of detritivores and planktivores early in the season maintain high densities of generalist predators, which

are then able to suppress pest populations on rice later in the season.

Trophic cascades induced by spiders in a grazing food web via energy subsidies from a decomposition web will occur only if certain conditions are met: (1) Bottom-up control processes in the decomposition web must affect spider densities; i.e., spiders must be food-limited, and fungivores/detritivores must be readily consumed by spiders if numbers of the former increase; (2) Increased availability of prey in the decomposition web must not cause spiders to switch from feeding on herbivorous prey, or if such changes occur, the increased numbers of spiders must compensate for this dietary shift; (3) Spider-generated trophic cascades in the grazing food web must be strong enough to enhance crop yield.

No direct experimental evidence exists to support the hypothesis that energy subsidies from decomposition food webs enhance crop yield via multichannel omnivory in agroecosystems. In the absence of direct evidence, the only alternative is to evaluate the evidence that the proposed conditions for such a detrital subsidy are satisfied. Below we summarize briefly some of this evidence, which comes from a mixture of studies with non-agricultural and agricultural systems.

Evidence.—Field experiments have demonstrated that spider populations frequently are food-limited (Wise 1993). Although most studies have been conducted with grazing food webs, some experiments have demonstrated bottom-up limitation of spider numbers in decomposition food webs in non-agricultural systems (Spiller 1992; Chen & Wise 1999). The importance of Collembola numbers in influencing spider population dynamics is particularly crucial to the argument. Experimentally enhancing detrital input to the forest-floor increases densities of Collembola and other fungivores, which is accompanied by a doubling of densities of many families of spiders (Chen & Wise 1999).

Indirect evidence suggests that Collembola help maintain high densities of spiders and other generalist predators in some agroecosystems. For example, two species of wolf spiders in Swiss wheat fields feed predominantly on Collembola (> 35% of their diet) early in the season. As the season progresses, however, Lepidoptera larvae and cereal aphids gradually become the spiders' main prey

(Nyffeler 1982). Field experiments have demonstrated that carabids and spiders can limit aphid numbers in cereal crops (Chiverton 1986; Edwards et al. 1979). Although this pattern supports the hypothesis that a detrital subsidy promotes top-down control in the grazing food web, the relationship between decomposition and grazing food webs in cereal crops is likely complex. In addition to subsidizing spider populations and inducing trophic cascades, high numbers of alternative prey from the decomposition web might weaken such a cascade because some aphid species are low-quality food for spiders (Toft pers. comm.; Toft 1995); and spiders might shift from aphids to higher-quality alternatives. However, although spiders can develop aversions to low-quality prey, limited consumption of sub-optimal food provides nutritional benefits to these predators (Toft 1995). Hence spider predation on aphids at low prey levels, common early in the season, may limit aphid outbreaks if the presence of superior-quality prey boosts spider numbers enough to ensure that the overall impact of spider predation on aphids is high (Toft 1995). An additional complicating issue is the finding that not all Collembola are high-quality prey for spiders (Toft & Wise 1999a, b). Clearly more information is needed before accurate predictions can be made about the general impact of increased densities of Collembola and other fungivores/detritivores on the total predation pressure exerted by spiders on agricultural pests.

Increasing evidence suggests that spiders can depress densities of agricultural pests in several types of crop; however, effects on crop yield have not been widely documented. Enough evidence exists to implicate spiders as potentially important biocontrol agents to justify research into the question of whether or not a detrital subsidy could increase their effectiveness. No experimental evidence exists to support the prediction that such a detrital subsidy could be used to enhance the biocontrol effectiveness of spiders. Experimental studies are needed with agroecosystems in which a detrital subsidy is likely to have an impact. Below we discuss one such system.

Vegetable crops.—Field experiments of Riechert & Bishop (1990) have revealed that spiders can limit densities of pest insects in vegetable gardens. Their use of fencing to exclude spiders could have also reduced carabid

beetles, which are abundant predators in agroecosystems. We have recently expanded their experiments to examine explicitly the combined impacts of spiders and carabids, their separate impacts, and whether or not intraguild predation limits their effectiveness in biocontrol.

In one set of experiments we employed fence barriers, pitfall trapping and hand removal to reduce densities of ground spiders, foliage spiders and carabid beetles (Tuntibunpakul & Wise unpubl. data). In the first experiment, conducted in mixed-vegetable gardens, reducing spiders and carabids led to elevated densities of squash bugs in cucumbers and Colorado potato beetles (CPB) in potatoes. The presence of beetles and spiders marginally increased total cucumber yield, significantly improved the individual weight of marketable cucumbers, and marginally increased the yield of one of two varieties of potato. In an experiment conducted the following year, manipulating spiders and carabids in a garden planted solely in potatoes had no impact on densities of CPB, which were higher than the previous year, and did not affect potato production.

In another set of experiments, densities of wolf spiders and carabids were manipulated together and separately by continuously altering rates of immigration into fenced plots in conjunction with removal by pitfall trapping (Snyder & Wise in press). In the first year, simultaneously decreasing lycosids and carabids had no impact on pests or yield of cucumber in a spring garden; however, reducing colonization by spiders and carabids of a summer squash garden harmed squash production (Snyder & Wise in press). In the second year (unpubl. data) we manipulated immigration rates of lycosids and carabids both singly and together in order to separate their impact as biocontrol agents and to uncover effects of intraguild predation on their total biocontrol effectiveness. In the spring garden carabids did not affect cucumber production, but in the fall garden of squash they reduced squash bugs and increased fruit production. Lycosids increased cucumber production by feeding on striped cucumber beetles. In marked contrast, in the summer garden wolf spiders harmed squash production by causing an increase in squash bugs at the critical early stage of squash growth. This indirect negative effect of

lycosids likely was caused by their feeding on important insect predators of squash bug nymphs. In the summer gardens, allowing carabids to immigrate into the plots compensated for the negative impact of lycosids on yield, so that the combined effect of the assemblage of wolf spiders and carabid beetles was to increase squash production.

Thus spiders and carabids have the potential to depress pest numbers and increase yield in potatoes and cucurbits, but the pattern is complex. Densities of immigrating spiders and carabid beetles may not always be high enough either to reduce pest numbers or to lower them enough to improve yield. Furthermore, lycosids can substantially reduce crop production by preying on other predators of insect pests. Whether or not the enhancement of spider numbers will improve vegetable yield depends upon both the densities and phenologies of pests and other predators.

Enhancement of spider numbers, and the provision of alternative prey to reduce their feeding on other predators of insect pests, has the potential to increase the impact of spiders in vegetable systems. Providing straw mulch increases the density of spiders ca. 10× compared to plots with bare ground (Riechert & Bishop 1990; Tuntibunpakul & Wise unpubl. data). Similarly, the use of straw refugia in soybeans can dramatically elevate the abundance (20–30×) and diversity of resident spider fauna (Halaj, Cady & Uetz unpubl. data). Such effects could be due primarily to altered structure of the physical habitat; however, some of the increase in spider numbers could have resulted from an energy subsidy derived from the decomposition food web based on the added straw. This effect could be particularly important later in the season, after the mulch has partially decomposed, enhancing detritivore populations.

It would be worthwhile to devise field experiments in which the rate of input of detritus to the decomposition food web of vegetable gardens is explicitly manipulated in order to test the hypothesis that a detrital subsidy can enhance the biocontrol impact of spiders (Fig. 3). Increased detritus could improve plant productivity simply by providing more nutrients, so a complete test of the hypothesis would require documentation that the detrital subsidy does in fact cause higher spider numbers and higher densities of Collembola and other fun-

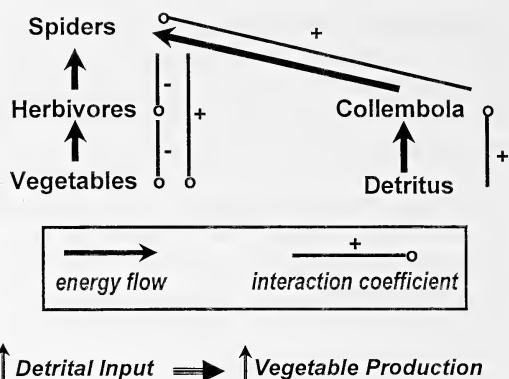


Figure 3.—Hypothesized increase in vegetable production via a detrital energy subsidy of a grazing food web in which spiders are top generalist predators.

givores, and that increased productivity of marketable vegetables can be explained as the result of decreased feeding by insect pests. The impact of a detrital subsidy could be investigated most directly by experimentally introducing high quality detritus to the system (e.g., Chen & Wise 1997, 1999). Support of the detrital-subsidy hypothesis would then justify detailed studies of how farming techniques could be modified to encourage the decomposition food web in vegetable production.

CONCLUSIONS

In theory, spiders have the potential to enhance productivity by increasing rates of mineralization through cascading top-down effects on rates of decomposition. Such cascading indirect effects are most likely to be of significance in no-till and conservation tillage farming. The actual impact of spiders on mineralization rates is difficult to predict. It is possible that spider predation also could negatively impact the rate of litter decomposition, as has been demonstrated for grassland systems. Such an effect might lower rates of plant production, but the expected time lags suggest that the overall impact of spiders on plant production will be determined more by their interactions in the grazing food web.

It is more likely that bottom-up control processes in the decomposition web can affect crop productivity via multichannel omnivory. Energy subsidies from the decomposition subsystem may cause spider-induced trophic cas-

acades that are strong enough to increase crop production. This conjecture remains a hypothesis, but well worth testing in agroecosystems in which detritus-based food webs can feasibly be enhanced.

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ARCHITECTURAL FEATURES OF AGRICULTURAL HABITATS AND THEIR IMPACT ON THE SPIDER INHABITANTS

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ABSTRACT. The density and diversity of the spider community has been closely tied to the structural complexity of the local environment. For instance, soil dwelling spiders increase dramatically when the litter layer is enhanced because there are more retreats and hiding places and because temperature and humidity extremes are moderated. Web-building spiders are directly linked to the configuration of the vegetation because of specific web attachment requirements. Both correlative and experimental data support a tight relationship between spider density and habitat structure. Most of the available data show that agricultural practices which enhance the structural complexity of the environment (such as intercropping, mulching, and conservation tillage practices) enhance the density and diversity of the spider community. The key question regarding spiders in agroecosystems is, of course, whether they are in any way suppressing the activity of herbivores. Some studies uncovered a strong link between habitat complexity, spider abundance and plant productivity; but others have not, and the mechanisms by which spiders could exert a top-down effect are not clear. More investigation into the specifics of how habitat structure influences the predator-prey interactions in agroecosystems is needed in order to truly understand and manage agricultural production in a responsible manner.

Some of the earliest studies of spider habitat selection and community structure focused on the importance of architectural features of the environment. Clear relationships have been revealed between the physical complexity of the environment and spider abundance and diversity both across successional gradients (Lowrie 1948; Barnes 1953; Duffey 1978; Hurd & Fagan 1992) and across geographical regions (Greenstone 1984; Rypstra 1986). Surveys as well as manipulative studies have demonstrated that spiders respond to the diversity and complexity of the vegetation (Rypstra 1983, 1986; Robinson 1981; Greenstone 1984; Gunnarsson 1990; Halaj et al. 1998) and that cursorial spiders, in particular, respond to the depth and complexity of the litter layer (Uetz 1976, 1979; Bultman & Uetz 1982, 1984; Hurd & Fagan 1992). As pointed out by Uetz (1991), there are several reasons why spiders should be more sensitive to structure than other organisms. As a group, spiders perceive their environment using vibratory cues which are mediated through the substrate on which they live. Web spiders must anchor their prey capture device to the appropriate

substratum and complex habitats provide appropriate sites for a greater range of sizes and types of webs. Finally, since all spiders are predators that can potentially consume one another, the extent to which they can coexist may strongly depend on their ability to move around and hide in a complex environment.

The literature on the responses of individual species of spiders and the community as a whole to habitat structure and complexity was comprehensively reviewed in the early 1990s (Uetz 1991; Wise 1993). The conclusions of both of these reviews suggest that, although clear associations exist, the specific aspects of the environment to which the spiders respond have not been adequately teased out. Diverse habitats provide a greater array of microclimate features, alternative food sources, and a greater number of possible retreat sites that can encourage colonization and the establishment of robust populations. More specifically, plant diversity and plant composition may influence predator diversity by changing foraging efficiency (Strong et al. 1984; Andow & Prokym 1990) and/or the nutritional quality of the herbivore prey (Price et al. 1980). Varia-

tions in the manner in which habitat structure affect interactions between predators and prey limit our ability to make broad generalizations regarding the specific mechanisms by which habitat diversity influences the spider community.

Numerous ecological models suggest that diverse producer communities will support more diversity at higher trophic levels. A recent study of Siemann (1998) demonstrates how complex testing this concept can be. He studied grassland communities with historical differences in fertilization into which he nested a more recent fertilization treatment. Past fertilization caused more than a four-fold decrease in plant species but resulted in no detectable differences in herbivore or detritivore species richness. Interestingly, arthropod predator (including spider) and parasite species richness was significantly higher in these plots. Siemann (1998) suggested that the predators might have become more abundant because they were more successful in foraging in the physically simpler environment but also mentioned that the shift in producer species composition may have changed the nutritional quality of the herbivores for the predator. This example runs counter to generalizations traditionally made by spider ecologists about the response of spider diversity to increased plant diversity (Uetz 1991; Wise 1993 and references therein). Siemann's results (1998) challenged our prior conceptions further in that his more recent fertilization treatments increased the diversity and abundance of all trophic levels in the grasslands. In this case, he explained the increase in herbivores and detritivores by suggesting that the increase in plant productivity allowed rarer species to persist. However, it is not at all clear why his two fertilizer treatments, which produced differences in the plant, herbivore and detritivore communities, had no apparent impact on predator diversity and/or abundance. Obviously the interactions in this trophic web cannot be explained by the basic principles we think we understand regarding how arthropod predators, including spiders, respond to habitat complexity. The only way to truly understand the responses of the predators in Siemann's (1998) experiments is to focus more directly on how the specific interactions between predators and their prey are mediated by the plant community.

Studies such as Siemann's (1998) may

serve to make us more pessimistic regarding our ability to predict the potential impact of shifting agricultural practices on predatory arthropods. Since more than half of the predatory fauna in agroecosystems are spiders (Ferguson et al. 1984; Young & Edwards 1990), and it is known that changes in spider density can impact pest populations (Mansour et al. 1983; Riechert & Lockley 1984; Nyffeler & Benz 1987; Nyffeler et al. 1994), it would seem logical that the spider community would be a key component of integrated pest management strategies. Even though significant control of prey populations by assemblages of spiders has been suggested repeatedly (Clarke & Grant 1968; Riechert & Lockley 1984; Chiverton 1986; Agnew & Smith 1989), pest control strategies in North America rarely include them (Young & Edwards 1990). In order to increase the emphasis on spiders as agents of biological control, it is imperative to decipher exactly how shifting agricultural practices that change the habitat structure within relatively homogeneous fields influence the density, diversity and foraging behavior of spiders.

Although the agricultural literature was not specifically addressed in the reviews of Uetz (1991) and Wise (1993), a rich body of work has demonstrated that vegetation diversity of agroecosystems provides some measure of plant protection (Risch et al. 1983; Andow 1991a). Root (1973) proposed two hypotheses to explain the lower levels of herbivorous insects and pest damage in diverse systems. The resource concentration hypothesis suggests that specialist herbivores respond strongly to homogeneous systems of their host plant and cannot reach high levels in diverse systems. More critical to arachnologists is the enemies hypothesis which suggests that predators and parasites are more effective in diverse systems where alternative prey are present. Apparently the idea that biological diversity promotes community stability (the diversity-stability hypothesis of MacArthur 1955; Elton 1958) captured the attention of agriculturists studying the response of arthropods to diversity (Goodman 1975; Risch et al. 1983; Coll & Bottrell 1995). Thus, the notion that habitat diversification impedes the build up of pest populations became a paradigm even though empirical evidence in support of it is not any more rigorous than the identification of the

specific features of a complex habitat to which the spider community responds.

Although the tendency over recent decades has been toward the simplification of the agricultural landscape, diversification within agricultural fields can easily be attained by intercropping, cover cropping, changing planting strategies and tolerating weedy culture. Overall, these practices tend to increase predator abundance (including spiders) and thus provide support for the enemies hypothesis (Ferguson et al. 1984; Coll & Bottrell 1995; Rypstra & Carter 1995; Balfour & Rypstra 1998; Costello & Daane 1998). However, it is not clear whether vegetation that provides abundant resources will act as a source or a sink for natural enemies in agroecosystems (Bugg et al. 1987; Kemp & Barrett 1989; Corbett & Plant 1993; Coll & Bottrell 1995; Costello & Daane 1998). For example, the greater availability of alternative food sources may reduce predation rate on a target pest (Ables et al. 1978). Non-host plants and high structural complexity may interfere with predator movement and alter the interactions between natural enemies and their prey (Perrin 1980; Andow & Prokym 1990). Alternative crops or weeds may actually draw predators away from the crop and thus reduce their impact on the herbivores (Bugg et al. 1987; Kemp & Barrett 1989; Rodenhouse et al. 1992). The specific manner in which diverse agricultural systems impact natural enemies in general or the spider community in particular needs to be quantified. Only then can we begin to make predictions about how the habitat changes that accompany diversification affect the role that spiders play in the food web.

There are a few examples of habitat manipulations in which the spiders appear to exert a top-down effect in the food web and increase plant production. In 1982, a USDA report mentioned that farmers in the Hunan region of China used straw bundles as retreats for spiders during irrigation of rice fields and that this minor habitat manipulation was associated with a 50-60% reduction in pesticide use. Kobayashi (1975) provided alternative prey in the form of fruit flies for spiders inhabiting rice paddies and observed an increase in spider populations and a decline in rice pests. However, the decrease in pest insects apparently came too late in the season to af-

fect the amount of damage experienced by the plants.

Critical experiments regarding the importance of habitat manipulations to spiders were conducted in a mixed vegetable garden (Riechert 1990; Riechert & Bishop 1990). The habitat for the spiders was altered by adding mulch, which provides structure and moderates physical conditions for spiders. Prey density was altered by planting flowering plants that were meant to attract pollinators. These manipulations increased spiders densities, reduced pest insect densities, and led to reduced plant losses to herbivory. Further experimentation with spider removals and separation of the mulch and flower treatments demonstrated that the spiders that invaded the mulch were responsible for the observed increase in plant productivity (Riechert 1990; Riechert & Bishop 1990). Garden systems tend to be more diverse than standard agricultural fields and small scale manipulations such as the addition of mulch are relatively easy for motivated gardeners to implement if economic or production benefits were to be accrued. What is not clear from these experiments is the specific feature of the mulch (i.e., microhabitat moderation, structure, protection from predators, increased levels of prey, etc.) to which the spiders were responding.

Planting ground cover under emergent agricultural crops, such as vineyards and citrus groves, has been shown to increase spider abundance and diversity (Altieri & Schmidt 1985; Wyss et al. 1995; Costello & Daane 1998) but little effort has been invested in understanding how it affects pest control. Costello & Daane (1998) compared changes in the spider community in California grape vineyards with and without ground cover and attempted to relate it to the abundance and diversity of pest insects. Although there was no significant difference in the total spider abundance on vines with or without ground cover, *Trachelas pacificus* (Chamberlin & Ivie) 1932 (Araneae; Corinnidae), was significantly more abundant on vines planted with ground cover (Costello & Daane 1998). Even though Costello & Daane (1998) noted that *T. pacificus* is a major predator of the common leafhopper pests, they are pessimistic about the ability of ground cover to reduce pest populations by enhancing spider abundance. This question will not be resolved without a more mecha-

nistic approach to understanding the specific interactions among the species that inhabit the different components of the habitat. For example, more detail regarding the effects of multiple predators and how they might take advantage of the movement of potential prey between the vines and the ground cover plants might explain effects that are not obvious from descriptive information about the distribution of organisms. Losey & Denno (1998a; 1998b) have described a situation where the escape response of an aphid upon encountering a predator foraging up on the vegetation made it more vulnerable to another predator on the soil surface. It is these kinds of complexities that must be incorporated more explicitly into our attempts to understand how spiders in complex habitats affect the food web.

Recently tilled and planted fields are barren habitats that are inhospitable for many arthropods, including spiders, yet this may be a critical time for establishing a community of predators capable of impacting plant production. In the spring, many spider species are actively engaged in widespread dispersal (Bishop & Riechert 1990), thus habitat manipulations that make the fields more attractive to them at this time may be particularly critical. Carter & Rypstra (1995) attempted to encourage spider establishment by placing crates in soybean fields just after planting. Their idea was that these crates would provide shade and some habitat structure while the plants were still small and then, as the plants grew, the spiders would move out into the vegetation where their impact on pest insects would be greater. Although their crates were colonized by spiders, the predominant species in the crates was a species that is not naturally abundant in soybean fields; and there was no evidence that these spiders moved out of the crates after the plants were mature. Nevertheless, across three seasons the biomass of insects consumed by the spiders in the boxes was negatively correlated with the amount of herbivory experienced by adjacent plants (Carter & Rypstra 1995). In two of three years, the herbivory experienced by plants in the vicinity of the boxes was significantly lower than in the fields at large or in areas where spiders were systematically removed. Although this manipulation was rather artificial and unlikely to be practical on a large

agricultural scale, it demonstrates that small manipulations that enhance spider populations can have significant effects on herbivory in a conventional agroecosystem. However, it is again the case that no attempt was made to reveal the specific mechanisms by which the spiders interacted with the herbivores to cause the reduction in leaf damage observed.

Existing data provide strong evidence that simple habitat manipulations can affect spider populations and impact plant production in agroecosystems. Further experimentation must focus on how specific shifts in actual agricultural practices impact the spiders and, ultimately, the damage inflicted by herbivores. One example in which the aforementioned studies may be particularly applicable is the shift to conservation tillage (no-till) that has been occurring in North America over the last few decades (Sprague & Triplett 1986; Gebhardt et al. 1985; Ehrenfeld 1987). Fields managed under conservation tillage regimes experience lower levels of soil disturbance, which reduces erosion and allows the development of a much more complex litter layer (Gebhardt et al. 1985; Hendrix et al. 1986; Wardle 1995). Likewise, pressure to reduce the use of chemical herbicides may lead to increased invasion of weeds (Triplett & Lytle 1972; Wardle 1995; Pavuk et al. 1997). It is generally known that no-till fields support a more diverse resident arthropod community including pests and natural enemies (House & Stinner 1983; Stinner & House 1990; Tonhasca 1993). As mentioned above, spider communities respond to both soil litter (Bultman & Uetz 1982; 1984; Riechert & Bishop 1990) and plant diversity, including weed density, in no-till soybean systems (Rypstra & Carter 1995; Balfour & Rypstra 1998). Likewise, lower levels of insect damage have been observed in some no-till systems (House & Stinner 1983; Andow 1991b). Therefore, one would expect this to be a promising system, from both ecological and economic points of view, in which to study the impact of habitat changes on the spider community and how they may impact plant production.

Research needs to proceed toward developing a mechanistic understanding of how spiders and other natural enemies respond to specific habitat manipulations and how the habitat manipulations mediate predatory intensity. We need to uncouple the linkages be-

tween the structure itself and the specific features of the structure to which the spiders are responding so that we can quantify the ultimate effects on the food web. Although it is generally hypothesized that diversity enhances natural enemies by providing supplemental resources, few studies have actually documented this phenomenon experimentally. Given the variability of the community level responses observed, further investigations should incorporate a broad spectrum of specific effects such as the importance of spatial variation, changes in survivorship and fecundity, more detail on mobility and dispersal patterns, and the dynamics of the predator-prey interactions that occur within the agricultural systems (Corbett & Plant 1993). Only this level of comprehension will provide a basis for understanding the specific role of spiders in agroecosystems and ultimately enable us to predict the response of spiders to changes in agricultural practices.

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AN INDIVIDUAL-BASED MODEL FOR DISPERSIVE SPIDERS IN AGROECOSYSTEMS: SIMULATIONS OF THE EFFECTS OF LANDSCAPE STRUCTURE

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ABSTRACT. A general individual-based model of spiders in agricultural land was constructed. The populations of spiders were simulated on landscapes which were defined from a set of landscape descriptors based on a Danish agricultural landscape. These descriptors gave the types of habitats present in the landscape together with their area and a frequency distribution of the size of individual habitat patches. The agricultural land was divided into crop types each with its own array of crop managements which were considered to influence the spiders via mortality. The dimensions of the model are relatively large, with the spider population able to grow to a size of one million individuals and with a spatial resolution of 10^8 landscape units. The effect of altering the spatial organization of the landscape elements was investigated together with the influence of the size of fields in the agricultural landscape. Results showed that the spatial arrangement of landscape elements did not affect spider population sizes, but that the effect of increasing habitat patch size, whilst maintaining a constant habitat area, was to increase population sizes, especially where dispersal was minimal. Thus stochastic events (e.g., mortality and the placement of set-aside), were not significant factors in the simulation results. Simulation results indicated that the optimal dispersal strategy for spiders in this system was one of high juvenile dispersal, although the extent to which these results can be translated to other systems is not yet known. These results indicate the potential for using models of this type for theoretical investigations of the life-history strategies used by spiders, especially where landscape heterogeneity and limited dispersal ability could result in complex spatial dynamic patterns.

There is an increasing realization that landscape-scale perspectives are important when considering the ecology of organisms (Dunning et al. 1992; Kupfer 1995). However, this new perspective brings with it a number of problems, not least of these is the difficulty of integrating the bewildering variety of data required to interpret the responses of organisms at landscape scales. These data typically operate at a range of scales and across a range of disciplines. For instance, a model of a dispersive spider may have to take large-scale topography into account because of the long-distance dispersal possible, but may also need detailed information at a field-scale to determine the reproductive success or survival of the spider when not dispersing. In addition, weather, local management (such as grazing, plowing and spraying) and the spiders responses to these factors must be considered. In this way the disciplines of ethology and ecology meet and their respective scales need to be reconciled (Lima & Zollner 1996). When these two are combined it may be pos-

sible to wield considerable interpretative power through the use of computer simulation models which are capable of integrating the range of data and scales required to investigate the determinants of spatial dynamics and distributions in heterogeneous landscapes.

The typical agricultural landscape of western Europe is, for the spiders that live there, a patchwork of more or less ephemeral habitats of varying quality. Survival in such landscapes presents the spider with a problem of exploiting resources while conditions are good and minimizing the chance of being killed by agricultural operations. However, landscapes are highly variable and agricultural practices are ever-changing, thus prediction of the success of a spider population will depend upon the particular set of circumstances under consideration. To date, there have been attempts to model this type of system as a set of populations linked by dispersal. Topping & Sunderland (1994) used a two-dimensional system of 30×30 squares to model the landscape whilst Halley et al. (1996) used a one-dimen-

sional ribbon of fields. The one-dimensional ribbon was justified by the assumption that spiders always disperse on a scale which is much larger than one or a few fields, and hence local spatial influences will be negligible. However, many spiders do not disperse on these scales and so it is pertinent to ask what is the effect of landscape structure on spiders with restricted dispersal ability. There are two aspects to take into account. The first is the actual landscape structure. This was improved by Topping (1997) to include much more realistic structures by hand mapping the landscape two-dimensionally in units of 50×50 m. However, this technique is awkward to use; and it is very time consuming to develop standardized landscapes which are significantly different from each other. The second aspect is that it may be more realistic to consider spiders, not as populations arbitrarily classified as being within a man-made field, but as individuals which are free to move between these artificial population boundaries. Thus the power of the individual-based modeling approach is invoked to take individual variation and the influence of location into account (see DeAngelis & Rose 1992).

This paper presents a model which can be used to develop detailed individual-based simulations to predict the impact of land-use and structure on the dynamics of spider populations with differing life-history strategies. Since landscape structure is an essential element the model is designed to be able to create, automatically, different landscapes with the same basic landscape descriptors (e.g., mean field size and variance). The model is designed for maximum flexibility of life history and landscape structure and management. The simulations presented here do not fully utilize these options, but they illustrate the potential of the approach by investigating the interaction between spider dispersal strategy and landscape structure.

METHODS

Model overview.—The model was built using C++ and an object oriented approach; it is an i-state configuration model (Caswell & John 1992) with a discrete time interval. The time interval used in these simulations was one month. However, events involving the development of spiders occurring at a finer temporal resolution were incorporated by han-

dling these events consecutively. Hence the development of eggs is considered before the development of juveniles. Mortality and dispersal are also managed in the same way. As a result an individual egg could, under extreme conditions, develop into a juvenile, disperse, develop into an adult and then be killed all within the single time step. There are two main elements to the model, the landscape and the spider population:

The landscape: The model landscape has a resolution of $10,000 \times 10,000$ units and is built of rectangles of varying size and dimensions which are classified into different habitat types. The basic landscape used in this study is based on the landscape of Århus County in Denmark, which is probably typical of most of the intensive agricultural areas of north-western Europe. The landscape was constructed by first defining a set of landscape descriptors which were used to generate a landscape of a particular type. These descriptors list the number of different habitat types of which the landscape is comprised, together with the proportion of land area they cover and a statistical description of the frequency distribution of size of individual patches of habitats. These habitat types typically include urban developments, variously classified woodland, open water, agricultural fields and miscellaneous small or marginal habitats. Once the descriptors were defined, the landscape was constructed automatically by a model which randomly selects individual habitats (defined as rectangles) from the described distributions and fits these together to form a landscape. Once the pre-defined total area for a habitat type is reached no more habitats of this type are selected by the model.

At the end of this process the landscape consists of a patchwork of major habitat types, thus having an overall structure but little detail about the precise habitat types. This is remedied by a second set of descriptors. These descriptors sub-divide the major habitat classification into a sub-classification (e.g., agricultural fields will be allocated crop types). Again, the sub-habitat classification applied is based on the proportion of habitat occupied by that sub-habitat in terms of area. These sub-classifications can also be divided into management categories. For instance, each winter wheat field may be classified as one of up to 15 different management types

(combinations of different farming operations). At the level of management categories each habitat patch in the landscape will have a management code attributed to it for each month of the year. These codes will determine when agricultural events will occur. The landscape also simulates rotational set-aside which covers 7% of the arable area in Århus County. Each year, the model allocates set-aside fields randomly to the landscape until 7% of the arable area is covered. However, no field may be in set-aside for two consecutive years. Crop rotation is implemented in a similar way by changing the crops allocated to fields whilst still maintaining the same area cover for each crop. An internal clock is incorporated which allows the habitat patches to alter their properties at each time step, so as to simulate the management operations described for their particular management category and habitat sub-classification combination. Weather data were also incorporated on a monthly basis in the form of a mean temperature and mean number of calm days (as a measure of dispersal potential via ballooning). The landscape simulation therefore consists of habitat patches which have been classified into different vegetation and management types, as described by a set of varying monthly states. Thus landscape structure and heterogeneity can be easily controlled and varied tremendously, both spatially and temporally.

The spider population: The spider population modeled is, like a real population, comprised of individual spiders in various states of development. The model recognizes individual spiders in three distinct development stages: egg, juvenile, and adult. In order to reduce the number of computations, only female spiders are considered in the model. Thus the implicit assumptions are that male spiders are never a limiting resource and that they follow the same dispersal rules as the females. Each stage has its own behavioral rules which govern the behavior of the individual in the simulation (Table 1). Population development is controlled by these behavioral rules and by the landscape's time clock and landscape data. Once set in motion the individual spiders modeled in the simulation reproduce, disperse and die according to their behavioral rules and data which they gather from the landscape.

The model allows for a population size of

a total of eggs, juveniles and adults not exceeding one million individuals. In order to ensure that the population could not grow beyond this limit, parameters representing carrying capacities were scaled down in initial tests until simulated populations were of a suitable size (K_A & K_J , Table 2).

Parameterization.—*The landscape:* The basic landscape was created using statistics relating to Århus County, Denmark. Average weather parameters were obtained from Danish national statistics (anonymous 1997) and temperature data loggers operating at Rønde, Jutland. These weather patterns were incorporated as standard weather for all simulation years. Topographical data used to generate estimates of area coverage for lakes and forests were available from the Århus County administration. Urban area sizes were estimated from human population census data by regression against the area of 31 towns and villages for which area data were available (regression equation $\text{km}^2 = 0.0005x + 0.0433$, where x is the human population; $P < 0.0001$). Field size data were obtained from ongoing agricultural studies in Denmark (T. Dalgaard pers. comm.). The area covered by agricultural crops was available from Danish National Statistics (anonymous 1996). Typical crop management for the area was obtained from Danish agricultural advisors. These standard parameters were used to build the standard landscape, 'Landscape 1.'

The spiders: The spiders modeled in this study were designed to represent a generalized spider species of the type which commonly inhabits agricultural land in western Europe. Table 2 lists the parameters that are integral to the spider models and their functions. The parameter values relating to reproduction and development were based on studies of the linyphiid spider *Lepthyphantes tenuis* Blackwall (Topping & Sunderland 1994, 1996, 1998; Sunderland et al. 1996) and were of a fixed value throughout the study. Other integral parameters were used as variables in this study and thus took on values according to the simulation being undertaken. Thus, following Weyman et al. (1995), the probability that a spider will disperse under favorable conditions was held constant throughout the year, whilst weather conditions control the possibility to disperse at any given time (based on

Table 1.—Simulated behaviors of each spider life-stage modeled.

Egg	
Behaviors:	
<i>Develop:</i>	The egg develops according to the temperature experienced following a standard day-degrees equation using the stage specific parameter T_E .
<i>Mortality:</i>	Determines whether the egg dies using a probability given by the mortality probability M_E , and the probability of mortality caused by management of the habitat at its present location.
<i>Hatch:</i>	The egg hatches and becomes a juvenile.
Juvenile	
Behaviors:	
<i>Develop:</i>	The juvenile develops according to the temperature experienced following a standard day-degrees equation using the stage specific parameter T_J .
<i>Mortality:</i>	Determines whether the juvenile dies using a probability given by the mortality probabilities M_{J1} and M_{J2} (see Table 2), the density of population in the habitat patch the spider occupies (interpreted as a density above a threshold, K_A), and the probability of mortality caused by management of the habitat at its present location.
<i>Dispersal:</i>	Determines whether a spider will attempt dispersal based on the probability given by the dispersal motivation (W_J) and the prevailing wind conditions obtained from the landscape. If dispersal can occur then a new location is generated, based upon a random direction and a distance traveled. The distance traveled is obtained from a^2/D_J , where 'a' is a random number between 0 and D_J , and D_J is the maximum distance traveled by a juvenile spider. This equation results in a center-weighted distribution of spiders from a point source. Thus a spider has a greater chance of traveling a short distance than a large and may travel up to D_J units from its starting position.
Adult	
Behaviors:	
<i>Mortality:</i>	Determines whether the adult dies using a probability given by the mortality probabilities M_{A1} and M_{A2} (see Table 2), the density of population in the habitat patch the spider occupies (interpreted as a density above a threshold, K_A), and the probability of mortality caused by management of the habitat at its present location. In addition, the spider will die if it has no further reproductive potential.
<i>Dispersal:</i>	As for the juvenile but uses the adult-specific parameters D_A rather than D_J and W_A rather than W_J .
<i>Reproduction:</i>	Depending upon the time of year and adult density, the adult may produce one or more egg-sacs per month. Reproduction is density-dependent above K_A . The chance of an individual producing and egg-sac decreases linearly with increasing density until it is zero at $K_A \times 10$. The gradient of this relationship is given by the parameter B . Each egg sac is assumed to have a fixed number of eggs and there are a fixed number of egg-sacs possible per spider (assuming no premature mortality). Egg-sacs are deposited at the spider's current location. After producing an egg-sac the spider may disperse. The probability of dispersal here is separate from the normal course of dispersal and is controlled by another parameter (RS). Thus RS allows some flexibility in reproductive strategy by allowing a spider to either lay eggs in a single location or disperse before producing the next egg-sac.

mean wind speeds); however, this parameter was varied between simulations.

There were also parameters relating to the effect of management on the spiders. Potentially these parameters could be used to vary reproductive ability, dispersal ability and mortality; but in the simulations presented here only mortality and reproduction were directly

controlled by these values. Reproduction was controlled by a binary switch which prevented reproduction in urban, water and forest habitats. Mortality was varied with farming operation (e.g., 90% mortality was assumed as a result of insecticide application).

Simulations.—The simulations investigated variation in dispersal-related parameters

Table 2.—Parameters controlling simulated spider behaviours.

Parameter	Function
M_E	Monthly egg mortality
M_{J1}	Monthly juvenile mortality below K_J
M_{J2}	Monthly juvenile mortality above K_A
M_{A1}	Monthly adult mortality below K_A
M_{A2}	Monthly adult mortality above K_A
K_J	Juvenile density at which mortality becomes density-dependent
K_A	Adult density at which mortality becomes density-dependent
W_J	Juvenile dispersal motivation
W_A	Adult dispersal motivation
D_J	Juvenile maximum dispersal distance
D_A	Adult maximum dispersal distance
RS	Reproductive Strategy—the Probability of dispersal after laying eggs
E	Number of eggs per egg-sac
S	Number of egg-sacs per adult
B	The gradient of the linear relationship between density and reduction in probability of egg-sac production
T_E	Day degrees required before eggs hatch
T_J	Day degrees required before juveniles mature

over a range of landscapes with different structures and managements. The main landscapes considered were based on topographical and management information from Århus County in Denmark. Thus the basic landscape comprised of 78% agricultural land of which one third is grassland, the remaining 22% is forest of various types, water and urban area. Three values (maximum, minimum and mid-range), were used for five dispersal related parameters (reproductive strategy (RS), juvenile dispersal-motivation (W_J), adult dispersal-motivation (W_A), juvenile dispersal distance (D_J), adult dispersal distance (D_A)). All sensible combinations of the possible 243 combinations of these values were tested. Thus a zero dispersal motivation ability precluded the testing of dispersal distances of greater than zero. Testing of each combination was achieved by taking the mean population size during the last 15 years of simulation from 20 simulations of 20 years using the same parameters for the spider life-history and the same basic landscape (i.e., the first five years were ignored because of the potential variance from different starting positions at the beginning of the

simulation). Thus variation between runs was due to stochasticity in the model (e.g., dispersal decisions, mortality, the position of set-aside), and the starting position for each simulation (which was a randomly positioned population of 1000 adult individuals). All landscapes constructed for the simulation were constructed by the model randomly allocating the pattern of landscape elements. In all cases only the stated change was made to the landscape so all other landscape descriptors were kept constant. All landscapes produced were checked by eye for skewed distribution of field sizes (e.g., all small fields clustered in one corner), and those showing such distributions were rejected.

Simulations considered.—(A). The effect of varying agricultural field size whilst keeping other factors constant. Three mean field sizes were used, 2.6, 4.9, 8.7 ha respectively (Landscapes 1–3). In each case three replicate simulation runs were performed in order to establish the degree of between-run variation. For the overall comparisons, these runs were combined by taking means. (B). The effect of different landscape structures whilst maintaining the same management and area coverage of habitats. Landscapes were re-created to give approximately the same mean field sizes and habitat coverage as Landscapes 1–3, but with a different spatial arrangement of actual habitat blocks (Landscapes 4–6). Again three replicate runs were combined for the overall comparisons.

RESULTS

Simulations.—Note that all population sizes given refer only to adults in the simulated population. The degree of between-run variation was minimal. Landscape 3 produced the maximal between-run variation (Fig. 1). Variation between runs of other simulations was negligible.

In all cases it proved impossible to reproduce exactly the landscape construction hence there was some variation in mean field sizes (2.7 vs. 2.8; 4.9 vs. 5.0; 8.8 vs. 8.9). However, the effect of recombining landscape elements but maintaining the same overall landscape structure was to produce little more variation than found between runs. Regression analysis produced slopes of 1.000, 0.999 and 1.008 for small, medium and large fields respectively

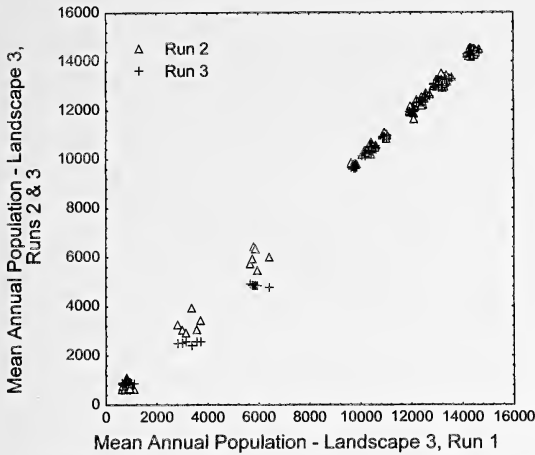


Figure 1.—The mean adult population size of two runs of the same simulation plotted against a third run. These simulations used 'Landscape 3' and resulted in the maximal between run variation of any simulations. This variation is caused by stochastic factors within the model not associated with landscape structure.

(all correlations $n = 147$, $R^2 > 0.999$, $P < 0.000001$).

Figure 2a, b shows the results of comparisons between simulation runs using landscapes with different mean field sizes compared to simulations using Landscape 1. As the field size increases so the departure of the curve from linear also increases. Four distinct life-history strategy groups can be identified (1–4, Fig. 2b). By examining the input parameters resulting in these four groups the following pattern emerged: *Group 1*: Low mean population level. In all cases there was little or no dispersal—either dispersal motivation or dispersal distance was zero for both adults and juveniles. Limited dispersal was only possible for some adults with an $RS > 0$. *Group 2*: Low to medium mean population levels. No juvenile dispersal, but adult dispersal distance > 0 . This group can be further sub-divided (into sub-groups 2.1–2.4), on the basis of increasing mean population size into four groups with the following pattern: 2.1 – $RS = 0$; 2.2 – $RS = 50$, $W_A = 50$; 2.3 – $RS = 100$, $W_A = 50$; 2.4 $RS > 0$, $W_A = 100$; *Group 3*: Medium to high mean population levels. Intermediate juvenile dispersal, i.e., $W_j = 50$. Within the group the trend is for decreasing adult dispersal ability with increasing mean population size. *Group 4*: High mean popu-

lation levels. High juvenile dispersal ($W_j = 100$). This group can be clearly sub-divided (into sub-groups 4.1–4.4), on the basis of increasing mean population size. 4.1 – $RS = 100$ or $W_A = 50$, $D_A > 0$; 4.2 – $RS = 50$, $W_A = 50$, $D_A > 0$; 4.3 – either $RS = 0$ or $D_A = 0$; 4.4 $W_A = 100$. Thus the groups of increasing population size also correspond to decreasing adult dispersal ability.

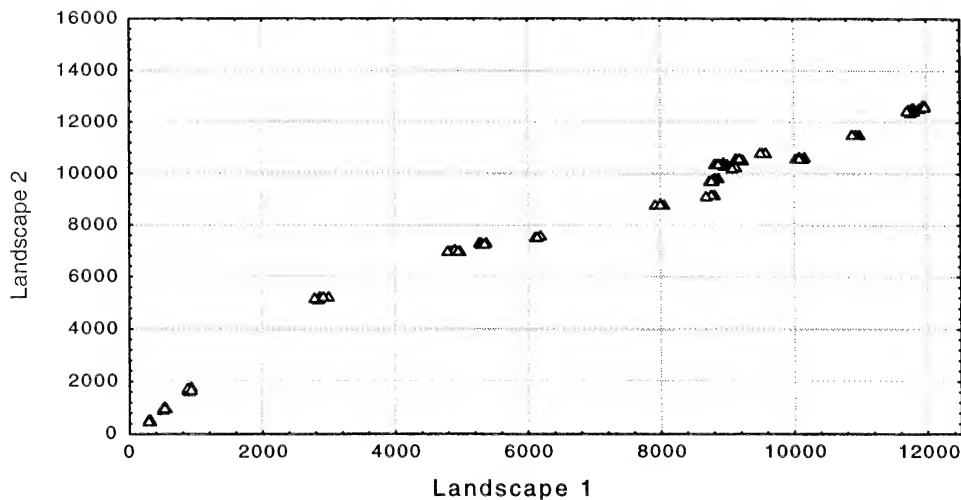
Increasing field size led to an increase in mean population size, but the increase was not linear. Group 2 was most strongly affected, especially sub-groups 2.1 and 2.2. Group 3 demonstrated considerable variation within the group whilst Group 4 responded linearly. The groups can be separated into two distinct parts (groups 1–2 and groups 3–4), on the basis of juvenile dispersal. Simulation results from Landscape No. 3 (large fields) show a distinct asymptotic curve over groups 1 and 2, but no such relationship for groups 3 and 4. There is a similar, but less pronounced pattern for Landscape 2 (medium-sized fields). Almost identical patterns can also be created by plotting the results of Landscapes 4–6 against Landscape 1, with Landscapes 5 and 6 similar to Landscapes 2 and 3, and Landscape 4 being only very slightly curved over groups 1 and 2.

DISCUSSION

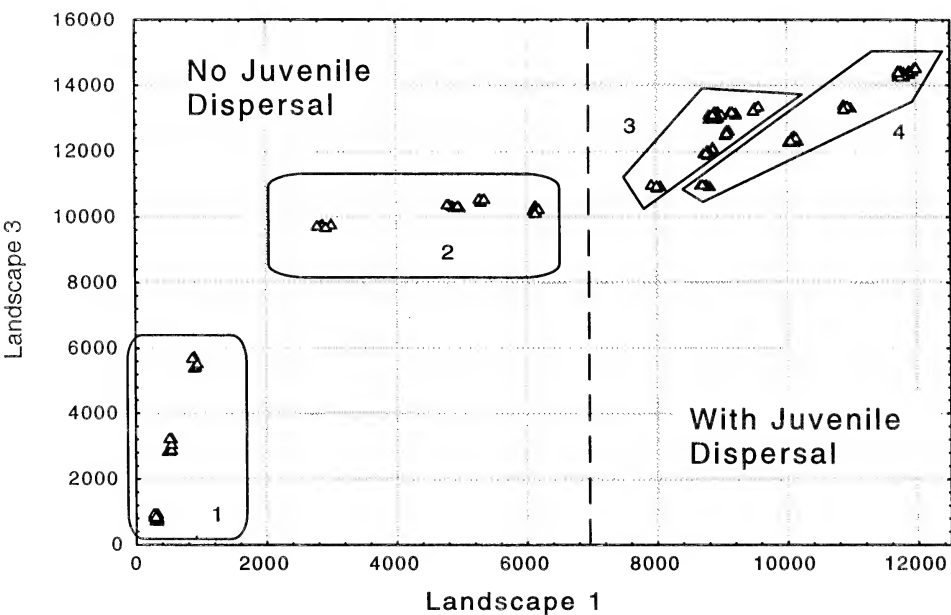
There was little between-run variation in mean population size when using the same landscape. This may not be too surprising because the differences between runs would be entirely related to stochastic events (e.g., mortality and the placement of set-aside). However, it does demonstrate that this stochasticity is not a significant factor in the simulation results. The variation in model output between different landscapes with the same basic configuration was also rather limited. The exact spatial relationship between habitat patches was not therefore significantly influencing the outcome of these simulations.

The effect of varying field size was, however, much more noticeable, especially for those simulations where there was no juvenile dispersal. In these cases the effect of increasing field size was to preferentially increase the population means for those simulations where adults could not disperse between egg-laying ($RS = 0$, Group 2.1) and those simulations where the only dispersal possible was due to

A.



B.



Adult dispersal ability:



Figure 2.—The mean adult population size resulting from simulations of two landscapes plotted against the results from the standard landscape ‘Landscape 1’ with small field sizes. Deviations from a straight line with a slope of 1 indicate an interaction between landscape structure and life-history strategy. A. ‘Landscape 2’, medium fields size. B. ‘Landscape 3’, large field size. Numbered boxes refer to groups of results (see text). Arrows show the direction of change in the magnitude of adult dispersal within the groups indicated.

RS (some of Group 1). In the most extreme case (low adult and no juvenile dispersal), the population increase was 400%. At first sight this seems like a counter-intuitive result. If increasing adult dispersal increases population size, then increasing field size should reduce the population because it effectively reduces the chance of dispersal to other habitats. But there are three interacting factors here: the patch, the effect of density and the ephemeral nature of the suitable habitats. The spider populations in the fields are always being reduced to low levels and then increasing again. When calculating the effect of density, the model assumes that spiders in a field space themselves more or less evenly throughout the field, thus density is field population size divided by field area. Hence, density dependent effects can cause two fields, one small and one large both being re-colonized by the same number of colonists after a catastrophic event, to have different growth curves. This effect will result in a feedback loop if dispersal is low, because few small fields can be colonized. Those that are colonized will get a relatively high density of colonists due to the fact that dispersal is spatially local, thus initial density will be high, compared to the same dispersers dispersing into a large field. This high density results in a low rate of growth which will mean fewer colonists and so even more restricted spatial distributions. This behavior would not be exhibited by the spatially-simplistic population-based models of Topping & Sunderland (1994) and Halley et al. (1996). The implication of this effect is interesting if consideration is given to those life-history strategies with medium levels of dispersal. In these cases, for large fields, many variations in strategy (e.g., minimal adult and no juvenile dispersal compared with maximal juvenile and maximal adult dispersal) all result in approximately equivalent mean annual populations. However, the same strategies on a small-field landscape result in a $> 100\%$ difference in mean annual population size. For such species landscape structure could be very important.

In these simulations, juvenile dispersal is clearly the most important factor determining mean population size. In those simulations with juvenile dispersal there is a relationship between increasing juvenile dispersal ability and population size; however, within the

groups with juvenile dispersal (Group 3–4), there is a negative relationship between adult dispersal ability and population size. This suggests that *in this system* dispersal is generally a beneficial thing, but that it is not an advantage to over-disperse. For the simulations without juvenile dispersal, generally the more adult dispersal the better; but the response is curvilinear such that maximal adult dispersal results in only marginally larger populations than medium adult dispersal levels, especially when fields are large. This is almost the opposite to the strategy suggested by Van Wingerden (1980), who believed that the best colonization strategy was to disperse as mated females. However, in the case where juveniles could not disperse significantly, Van Wingerden's strategy matches the model results. It should also be noted that the results may change for simulations of other combinations of life-history parameters and landscape structures and managements. Hence, in agreement with the model results, high juvenile dispersal is the norm for most families (e.g., Dean & Sterling 1985). However, there are also significant differences between studies and families, for instance Duffey (1956) and Greenstone et al. (1987) found that in Linyphiidae there can be a relatively large proportion of adults dispersing by ballooning. This is almost certainly a contributory factor to the confusion around the causative factors of ballooning (see Weyman 1993). The choice of ballooning strategy will depend upon the particular situation under consideration, and the combination of factors needing to be considered results in a complex problem.

The model presented here is still in an early stage of development. In particular, more work is needed to determine how important the effects of spatial heterogeneity in the landscape are and how dividing the temporal aspects into even finer time steps might influence the model output. More importantly, an analysis of actual spider strategies might reveal constraints to the number of possible parameter combinations used. This would be particularly useful when considering varying developmental and reproductive parameters. Nevertheless, the preliminary results presented here suggest that this type of simulation modeling may render some of the complex aspects of investigations into the spatial dynamics of spiders more tractable than previously

possible. In particular, the two-dimensional nature of the model together with the individual-based approach permits the investigation of the effects of local conditions within a complex landscape. Such effects have not previously been considered in models of spiders in farmland.

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THE HOWS AND WHYS OF SUCCESSFUL PEST SUPPRESSION BY SPIDERS: INSIGHTS FROM CASE STUDIES

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ABSTRACT. We can identify agricultural systems in which spiders might best be applied in pest suppression from study of the mechanisms by which spider populations influence prey in natural ecosystems. Theory predicts that prey control is achieved through the development of a stable interaction between predator and prey populations. Two models have been applied to predator control of prey, limit cycle and equilibrium point or focal control. Limit cycle control is exerted on a prey species population by a predator species that tracks the densities of its prey. Although the limit cycle approach is commonly applied to pest control situations, the long life cycles and generalist feeding habits of spiders limit their abilities to exhibit density-dependent tracking of their prey. Crops with short growing seasons and species-depauperate systems are the best candidates for limit cycle influences of spiders on prey. Spider populations that exhibit an uneven age-structure and have strong migratory/aggregational tendencies would offer the greatest pest suppression in these simple systems. Equilibrium point/focus control involves the limiting effects of an assemblage of polyphagous feeders on an assemblage of prey species. Spiders fit this model to a greater extent than they do a limit cycle model of prey control. Agricultural systems that conserve spider densities and species representation through minimal chemical application and the maintenance of ground cover are good candidates for equilibrium point control of prey by spiders. It is also important to recognize that many success stories in agroecosystems do not involve stable interactions between predator and prey populations. Indirect effects (e.g., the cessation of feeding in the presence of a predator) and superfluous killing of prey are two factors that augment the influence of spiders on targeted insect populations.

Field biologists search for patterns in natural ecosystems with the ultimate goal of applying the knowledge gained to human benefit. Of particular concern to the arachnologist is maximizing the potential of spiders to control insect pests in agroecosystems. Wang (1982) reports that as long as 2000 years ago, Chinese writing states that “If there is a large gathering of spiders, everything will be satisfactory.” This contribution deals with how spider abundance and the mechanisms of prey control they exhibit affect their influence on prey populations in natural and agricultural systems.

SPIDER SIGNIFICANCE IN NATURAL ECOSYSTEMS

Energy and nutrient flow studies.—One problem inherent in assessing the predatory role of spiders is the logistical difficulty of determining not only what spiders eat, but in what quantities relative to other predators in a system. Our best estimates of spider significance in arthropod community dynamics actually are available from radioisotope tagging experiments completed on a reservation at the

Oak Ridge National Laboratories in east Tennessee (van Hook 1971; Moulder & Reichle 1972). Van Hook (1971) identified wolf spiders of the genus *Lycosa*, (i.e., *Hogna* and *Rabidosa*) as the most important predators of herbivorous insects in the *Festuca-Andropogon* old field system he analyzed. These lycosids were prominent throughout the plant growing season, while other biomass prominent predators (i.e., other Araneae) were most important only in spring and early summer. Van Hook attributed 21.1% of the total mortality of herbivorous insects (i.e., orthopterans, hemipterans and homopterans) to predation by *Hogna* and *Rabidosa* wolf spiders. (Actually, the percentage of consumer biomass cycling through the two spider populations was underestimated in the study, because insect exuviae and egg clutches were included as part of the estimate of mortality attributed to non spider sources (van Hook 1971). Spiders in this grassland ecosystem exhibited a mean density of 56 individuals/m² and a mean biomass of 146 mg/m²; other arthropod predators in the system “were not present in sufficient

biomass to warrant consideration" in van Hook's (1971) analyses.

Moulder & Reichle (1972) followed the movement of the radionucleotide, cesium-137, through cryptozoan food chains on the laboratory's reservation. Forty spider species were represented in the samples collected from the litter community. They exhibited a mean density of 126 individuals/m² and a dry weight biomass of 43 mg/m². Thus the greater spider densities in this system compared to the grassland system van Hook (1971) investigated were offset by the smaller sizes of individual spiders. Centipedes (Chilopoda) and predaceous beetles (Coleoptera) were the other numerically and biomass prominent predatory groups in the forest floor community. Spiders, however, were both numerically more abundant (2.7 times that of either the centipedes or the predaceous beetles) and had a total biomass that was 1.4 times greater than the other classes of invertebrate predators. Moulder & Reichle (1972) attributed the numerical and biomass prominence of spiders in the forest floor system to their greater predatory effect on herbivorous insects: spiders consumed 77.8% of the herbivorous prey biomass lost to predation, while centipedes consumed 14.6% and coleopterans 7.7%, respectively.

Allochthonous food sources.—The two classic studies described above are representative of the field of ecology that deals with the cycling of energy and nutrients through the ecosystem, consisting of both biotic and abiotic components. Ecosystem ecology's interest in top-down effects and trophic cascades (e.g., Hairston, Smith & Slobodkin 1960; Cohen et al. 1990; Hunter & Price 1992) has led to another example of the relationship between spider abundances and their effects on prey populations in natural systems. There is no general agreement as to the relative importance of top-down versus bottom-up control of food-web structure. Rather, the type of control appears to be system dependent. Polis & Strong (1996) proposed that trophic cascading (top-down effects) is most pronounced where there is an allochthonous source of food to predators. They argue that external food inputs will augment predator numbers to the extent that they can impose control on the lesser abundant resident prey and thus have cascading effects on the plants that these primary consumers forage

on. In Polis & Hurd's (1995) island food-webs, beached marine algae and carrion supported extremely large populations of arthropod detritivores. The detritivores, in turn, provided more than 90% of the food to spider populations of sizes that were 1–2 orders of magnitude greater than those observed for similar areas not influenced by the detritus. These large populations of island spiders strongly limited terrestrial herbivorous insects and the plant damage they would ordinarily have imposed. Henschel et al. (1996) suggest that emergents from aquatic habitats can have a similar subsidizing influence on spider populations. They found that spider community richness and biomass are significantly higher in the vicinity of water bodies with emergent insects than in comparable habitats away from water bodies. The authors conclude that such subsidies might be used to augment the role of spiders in agroecosystems.

POTENTIAL MECHANISMS OF SPIDER PREY LIMITATION

Non-consumptive effects.—In managing populations of pest insects and the damage they impose on crops, practitioners are interested in predator control of prey. Modeling approaches indicate that prey control by predators is achieved when a stable equilibrium is established between predator and prey population numbers. In practice, successful control commonly violates the assumptions of a stable equilibrium (Murdoch et al. 1985). 'Predator-induced effects' and 'superfluous killing' are two effects that spiders may have on prey population dynamics that fall outside of stable population interactions as they are non-consumptive effects. Predator-induced effects occur as a consequence of the fact that predators and prey are in an escalating evolutionary race. Predators become increasingly more efficient at capturing prey, while prey have evolved responses to predatory cues that permit escape from predation. Predator presence thus causes pests to cease feeding, to forage at less favorable sites, and to drop off host plants altogether in an escape response. The resulting effect is usually a slowing of prey population growth, which delays the outbreak phase. However, dropping from a plant to the forest or field crop floor may result in mortality as well due to desiccation and predation by generalist predators (ants and spiders in the

case of the hemlock woolly adelgid (McClure (1995)). Nakasuji et al. (1973) document the significance of predator-induced effects by linyphiid spiders on tobacco cutworm larvae, *Spodoptera litura*, by comparing spider exclusion cages to open cages. Only 4% of the 60% mortality rate suffered by cutworm larvae was attributed to actual spider predation, another 18% was not related to spider causation, and 38% involved predator induced effects (i.e., larval dispersal/dislodgement from the foraging site caused by spider presence). Since there is no ground cover in tobacco, dislodged larvae suffered starvation (Nakasuji et al. 1973).

There is evidence that trophic cascades can also be elicited through indirect predator-induced effects in which herbivores shift their foraging behavior in response to perceived predation risk. Schmitz et. al. (1997) found that 'risk' spider treatments (glued chelicerae) elicited similar avoidance behavior by grasshoppers feeding on herbaceous plants and grasses in an old field as did 'predation' (intact predators) spider treatments. Both treatments decreased the impact grasshoppers had on grass biomass, evidence for the existence of a trophic cascade in each case.

Superfluous killing, also referred to as wasteful killing and overkill, entails capture rates that significantly exceed rates of consumption: it includes the partial consumption of multiple prey items and the killing of prey that are never consumed at all. Samu & Biro (1993) observed killing without feeding and partial consumption of prey in the lycosid, *Pardosa hortensis*, when they offered test subjects high prey densities. Riechert & Maupin (1998) also observed high levels of these two facets of superfluous killing in all of the web spider species they tested: the theridiid *Achaeearanea tepidariorum* (61%), the araneid *Argiope trifasciata* (49%), the dictynid *Dictyna volucris* (20%), the agelenid *Agelenopsis aperta* (44%), and the linyphiid *Florinda coccinea* (43%). The numbers in parentheses following the test species names refer to the proportion of prey captured that were not consumed. Thus spider killing of prey was between 1.2 and 2.6 times greater than that required for feeding.

Combined then, predator-induced effects and superfluous killing can account for in excess of 80% of spider limiting effects on prey

populations. These kinds of non-consumption influences must be considered in assessing the impact of spiders on pests in agroecosystems.

Equilibrium models of predator-prey interactions.—In the reductionist approach commonly applied to agroecosystems, there is an interest in dealing with a single pest species problem. The addition of a single predator or parasitoid species to control a particular pest is an attempt to establish a stable limit cycle between predator and prey population numbers (Hassell 1978). This reductionist approach involves the tracking of the size of a prey population by the selected predator/parasitoid population. Density-dependent tracking requires that the predator/parasitoid: 1) have a life span of similar length to that of its prey, 2) is a prey specialist, and 3) exhibits a search behavior pattern that concentrates foraging in patches of high prey densities while allowing prey refuges to survive (Hassell 1978; Murdoch et al. 1985).

In the food-web literature, top-down control and trophic cascades are achieved through another model involving stable predator-prey population interactions, stable equilibrium point or focal control. In this mathematical model, population sizes of predators and prey equilibrate at some relative level rather than cycling out of phase of one another, which is characteristic of limit cycle control (DeAngelis et al. 1975; Tanner 1975). To achieve a stable equilibrium, there must be one or more polyphagous predator populations and an assemblage of prey types. As predator encounter rates with prey change in space or time, individual predators will switch feeding concentration among these prey types (Murdoch & Oaten 1975; Beddington et al. 1978). In addition, the predators must not be limited by local prey availabilities in the immediate sense. Rather, they are expected to have some mechanism of self-damping that keeps their population numbers below the limits of prey availability (e.g., energy-based territoriality, cannibalism or forced migration) (DeAngelis et al. 1975; Tanner 1975; Post & Travis 1979; Erlinge et al. 1984). These behaviors often are evolutionarily adjusted to averages or lows in prey availabilities for particular habitats (e.g., the funnel-web spider, *Agelenopsis aperta* (Riechert 1981)).

IMPLEMENTING SPIDER CONTROL IN AGRICULTURAL SYSTEMS: THE NEED FOR SYSTEM SPECIFIC PROTOCOLS

Single spider species on single pest species: limit cycle control.—Many pest insects are *r*-selected and thus have short generation times and high reproductive potentials. Because spiders have much longer generation times and comparatively low fecundities, they generally will not develop stable limit-cycles with their insect prey. It may be possible to achieve stable cycling between a spider species and a particular pest in a simple system with just a few herbivores and/or a crop with a very short life cycle. An uneven age distribution exhibited by a spider population (e.g., the multivoltine lycosids (e.g., *Pardosa lugubris* (Walckenaer): Edgar 1971) and linyphiids (e.g., *Erigone arctica* (White): van Wingerden & Vugts 1974)) and a strong aggregational numerical response to prey densities (e.g., aerial ballooning by linyphiids in response to localized weather conditions and densities; see review in Riechert & Gillespie (1986)) would also permit some density-dependent tracking of the prey population by a spider species population. There would be fewer generations of pest population build-up in the short-season crop, and the predators would be concentrating foraging on encounter with the numerically prominent prey, the pest.

Obviously, the best case scenario for successful control by limit cycle would involve spider species with the characteristics listed above feeding on a pest in a crop with a short life cycle. An example of a system that meets the short-crop season criterion is spring barley in Sweden. Chiverton (1986) found that linyphiids successfully control cereal aphids, *Rhopalosiphum padi*, in this northern region because *R. padi* overwinters here only in the egg stage. The growing season is simply too short to permit the sowing of a fall grass or cereal crop that would permit the build-up of large *R. padi* populations of viviparae before spider emigration in May and June. Aphid densities in barley field plots enclosed early enough to prevent spider emigration were six times higher than those observed in unenclosed plots in Chiverton's (1986) study.

Spider species assemblage control of pest species assemblages: stable equilibrium point or focal control.—There are objective

reasons for implementing a holistic approach (stable equilibrium point or focus control) to pest suppression by spiders as opposed to the reductionist approach, a single predator species acting on a single pest species (limit cycle). Stable equilibrium point control or focus (Tanner 1975) is the predator-prey model that is associated with top-down and cascading effects in natural food webs (Post & Travis 1979) and spiders exhibit the traits requisite to stable equilibrium point control of prey by predators (Riechert et al. 1999). They are, in fact the prominent predators of insects in natural ecosystems and this occurs despite the fact that they are self-damped by territorial and cannibalistic behaviors (Edgar 1969; Riechert 1981; Wagner & Wise 1996). Self-damping behavior is actually a necessary condition of stable equilibrium-point control of prey by polyphagous predators. Thus spiders are well-suited to this community level approach to prey control. In addition, the fact that suppression of a prominent pest is often followed by new problems with secondary pests favors a community approach where an assemblage of predators influences the entire assemblage of pest species in a local system.

An example of a holistic approach to pest suppression by spiders is offered in Riechert & Bishop's (1990) study of spider assemblage effects on herbivorous insects in mixed vegetable garden systems. Riechert and Bishop observed a highly significant spider assemblage effect on pest insects (60–80% reduction in pest-induced plant damage) across a wide variety of vegetable types. The effect was achieved by grass-hay mulch applications, which augmented spider population densities thirty-fold over those observed in tilled control plots. Contrasts completed on spider predation effects in the mulched plots indicated that spiders significantly suppressed insects and thereby afforded less plant damage in mulched than in bare-ground control plots. On the other hand, pest numbers and plant damage were not significantly different between controls and mulched plots from which spiders were systematically removed.

Although the analysis of variance was completed on spider densities alone, Riechert & Bishop (1990) presented additional analyses of the quadrat sampling of spiders as well as the results of timed watches of foraging activity within the same system. Calculations made

on the data set from the quadrat sampling produced an average spider diversity (Shannon-Wiener H') in the tilled control plots of 0.94 compared to an average of 2.48 in the mulch and mulch + flowers plots (Pielou 1974). In a five guild system, the nocturnal running spider guild was totally absent from the tilled control plots, while all guilds were well represented in the mulch and mulch + flowers plots. Fifteen families of spiders were observed during the course of the foraging observations, six of which were web-building families. Most of the spider families were observed feeding on more than one pest species with six families feeding on almost the entire range of 13 insect pests observed during the course of the watches. Riechert & Bishop (1990) conclude from these results that the significant effect of spiders on pest insects in the mixed vegetable system was an assemblage effect, rather than the effect of just a few prominent spider species.

Augmentation: sheer numbers versus species richness.—Regardless of the mechanisms by which control is achieved, all evidence indicates that successful pest suppression by spiders will best be achieved through the maintenance of high spider densities and in many cases also high species diversities. Maximization of spider densities and species richness are steps that logically must be taken in agricultural systems to increase the beneficial functioning of spiders in them.

Numerous studies support the idea that spider effects on prey are approximately a function of spider versus prey densities/biomasses in a system (e.g., natural communities: Moulder & Reichle 1972; Polis & Hurd 1995; Henschel et al. 1996; Kajak 1997; coconut: Sathiamma 1995; corn: Laub & Luna 1991; Clark et al. 1994; Coll & Bottrell 1995; cotton: Sterling et al. 1989; mixed vegetables: Riechert & Bishop 1990; old fields: Riechert & Lawrence 1997; pastures: DeBarro 1992; rice: Sasaba et al. 1973; Wang 1982; Orazé & Grigarick 1989; Litsinger et al. 1994; soybeans: Carter & Rypstra 1995; wheat: Hausamman 1996). The significance of increasing species diversity is less clear. From summary analyses of the performance of prominent single spider species versus spider species assemblages, Provencher & Riechert (1994) and Riechert & Lawrence (1997) in different experiments found that more than 70% of total reduction

in prey biomass and numbers (over that exhibited in spider removal controls) is contributed by single spider species. This would seem to indicate that having different foraging strategies represented is less important than mere numbers or biomass. However, Riechert et al. (1999) encountered very different results when they considered the predatory performance of spider species assemblages versus those of single prominent spider species over time (i.e., a four month period). The spider species assemblage was far more temporally consistent in its predation effects on the broad spectrum of prey types encountered in the old field system than was any single spider species (four numerically/biomass prominent species tested). Further, no single spider species performed as well over time towards a particular prey category as did the spider species assemblage, despite the fact that all of the predators used in the single species treatments were maintained at high densities throughout the four months of the study. Each spider species did show changes in linear dimensions, mass, and reproductive status that corresponded to its own unique life cycle at various times during the period of the study. Therefore, spiders show changes in their diets over time, a factor that makes it important to have a diversity of spider species in longer-lived crop systems.

Sathiamma (1995) reached a similar conclusion in a study of natural enemy suppression of the white spider mite, *Oligonychus is-eilemae* on coconut foliage (See also Agnew & Smith 1989 for spider suppression of pests in peanuts). The total predator density (seven prominent species) corresponded closely over time to the density of the mite and control was adequate to eliminate the need for chemical applications. No single predator, however, was abundant at all potential peak periods of mite density and Sathiamma concluded that the suppression effect of any single predator species by itself on the pest would be insignificant.

This is not to say that single spider species might not be able to exert sufficient control to eliminate the need for chemical intervention in some systems (see also section on limit cycle control). It may be that in exhibiting high population densities at critical times in the life cycle of a pest, a single spider population may suppress that pest sufficiently to require only

minimal chemical intervention during periods when the predator's life cycle is out of phase with the pest. Such a special case may account for the successful use of *Lycosa pseudoannulata* in controlling green rice leafhopper in Japan (Kiritani & Kakiya 1975). This predator imposes highly significant reductions of overwintering leafhoppers that prevent the early season transmission of rice diseases. A systems model has been developed that incorporates the densities of this predator and those of the pest in determining when particular paddies need to be treated with insecticides (Kiritani & Sasaba 1978).

It is important to note that while simulation models may key on the densities of prominent spider species in the management of a particular pest, it is probable that any conservation scheme designed for a prominent spider will also foster other spider species populations as well. While these other species might have lesser individual roles, their cumulative effect on pests and crop damage can be significant.

Spiders and agroecosystem practices.—Successes with spider suppression of pests in agroecosystems are correlated most frequently with increased predator densities, though recent studies indicate that species richness may be an important component as well. Augmentation of spider densities and accompanying species richness in agroecosystems could include the following three practices: 1) restriction of chemical pesticide applications to an as needed basis, 2) habitat diversification, and 3) maximization of allochthonous inputs.

1). Restriction of chemical pesticide use.—The literature on the deleterious effects of chemical insecticides on spider communities is too substantial to attempt to cover here. I include only two systems (rice and cotton) for which simulation models have been developed that favor the conservation of spiders through the monitoring of pest and predator ratios and selective use of pesticides where warranted. Spiders are used effectively in the control of rice pests in southeast Asia. Kiritani (1977) reported that the regular application of a broad spectrum insecticide to control a rice stem borer in Japan decimated spider populations but had little effect on the leaf- and planthoppers that transmit viral diseases in rice. It took ten years for the spider populations to sufficiently recover from exposure to the insecticide to be useful in suppressing the

major new problem of insect transmitted viral diseases. In China, Wang (1982) found that when spiders moved into an area of planthopper infestation, they reduced the pest: predator ratio from 9 to 1.5:1 within 10 days in one study area and from 5:1 to 0.03:1 within 5 days in another. After implementing conservation practices that fostered spider density increases (e.g., encouraging the movement of predators from early rice plantings to 2nd plantings and using cultural practices that limited the frequency of pesticide application and quantities of chemicals used), the need for chemical pesticides decreased as much as 80% with no measurable loss in rice yields. Monitoring programs of predator density/pest density ratios and weather are used in rice in Japan to determine when pesticide applications are required (Sasaba et al., 1973). A similar systems model has been developed for cotton by researchers at Texas A&M University (e.g., Hartstack & Sterling 1989; Sterling et al. 1992). The TEXTCIM model is widely used in Texas cotton to predict when it is economically beneficial to apply chemical insecticides rather than to rely on natural enemy (primarily spider) suppression of pests. Breece et al. (1990) tested the predation component of the TEXTCIM model for cotton, obtaining evidence that natural enemies protect the Texas cotton crop for 95% of the crop days, whereas chemical pesticides provide control for only 5% of the season (See also Mansour (1987) on spider control of cotton pests in Israel).

2). Habitat diversification.—This problem has been addressed in a number of ways, including the addition of weed strips, the maintenance of uncultivated borders, intercropping, and the application of mulch and other ground covers. The first three approaches have produced mixed results. Jmhasly & Nentwig (1996) report that the addition of weed strips to winter wheat did lead to higher web-spider densities in the vicinity of the strips, but that this increase did not lead to protection of the wheat crop from pest damage. Riechert & Bishop (1990) did not find that alternation of rows of vegetables with flowering buckwheat augmented spider numbers compared to bare-ground controls, nor was plant damage less in the plots containing the flowering buckwheat.

A potential increase in spider diversity is one pest suppression benefit of intercropping,

but this suppression effect may be confounded by the fact that intercropping also reduces oviposition sites for the pests. Roltsch & Gage (1990) report that tomatoes intercropped with beans in the control of the potato leafhopper, *Empoasca fabae*, did not increase natural enemy densities nor species richness, but nevertheless suppressed pest densities. The availability of oviposition sites was the important factor in this study. On the other hand, Coll & Bottrell (1995) found that spiders and nabid hemipterans had a greater effect on Mexican bean beetle (*Epilachna varivestis*) populations in dicultures of maize and bean vegetation than in bean monocultures. The lower bean beetle numbers were correlated with the higher abundances of the predators in the diculture.

The problem I have with all three of the above habitat management techniques concerns the question of whether the augmented spiders will move into the crop where the pest problem exists versus stay in more structurally complex natural habitats. Bishop & Riechert (1990) did not find that spiders from surrounding natural communities (i.e., old field, oak-hickory woods, and briar) colonized a mixed vegetable garden system. Over 60% of the species present in the garden system were not even collected in neighboring habitats and experimental limitation of ground dispersal indicated that most of the colonization occurred through ballooning.

Greater success has been achieved with the addition of ground cover and structure in annual crop systems (e.g., mulch in vegetables (Riechert & Bishop 1990), artificial habitat structure in soybeans (Carter & Rypstra 1995), and in no-till corn through the mowing of the winter cover crop (Laub & Luna 1991)). In the first two studies, experimental increases in spider densities and suppression of pest numbers and crop damage were noted. Laub & Luna (1991) found that by mowing a winter rye cover crop rather than spraying it at corn planting time, they achieved a significant net economic benefit (US \$91–\$113/hectare). They attribute the benefit of the mulch produced by mowing rye to suppression of army worm populations through the conservation of natural enemies in the mowed treatment. (Other work by this lab (Clark et al. 1994) used predator exclusion arenas in corn to demonstrate significant carabid and

staphylinid beetle, ant, and spider predation effects on armyworm damage.) The application of mulch to an agroecosystem early in the season may provide more favorable thermal environments to the spider populations before crop growth is sufficient to provide cover. It also may provide an abundance of early food in the form of subsidies from the detritivore food chain (e.g., collembola).

3). Maximization of allochthonous inputs.—It is clear from Polis & Hurd's (1995) study that allochthonous inputs from detritivore food chains may also subsidize spider population densities, permitting them to have greater cascading effects on crop production. Little is known about the detritivore community in temporary systems. Turnbull (1966) reported that 38% of the food of spider communities in overgrazed pastures was contributed by the detritivore food chain; and Kajak (1995) reports that linyphiid, araneid and lycosid spiders generally feed to a large extent on detritivorous dipterans. Sunderland (1975) and Sunderland et al. (1986) demonstrate the significance of the contribution of collembola from the detritivore food chain to linyphiid spiders in cereals. These serve as alternative food to polyphagous predators early in the growing season of the crop when pest numbers are low. The build up of the linyphiid populations supported by the collembola permits effective suppression of pest numbers later in the season when warm temperatures caused the collapse of the collembola populations and the predators switched to feeding on aphids.

Although De Barro (1992) does not directly address the role of detritivores in supporting spider populations in irrigated perennial pastures in Australia, this system too is likely subsidized by input from decomposer food chains. De Barro (1992) experimentally demonstrated that lycosids and linyphiids significantly limit the population growth of a prominent pest, the cereal aphid *Rhopalosiphum padi*, in its summer pasture refuges. The removal of spiders led to a 15–16 fold increase in *R. padi* numbers in experimental plots. The limiting effect spiders imposed on the aphids reduced the number of alates produced in the fall that could colonize and transmit diseases to cereal crops. *Rhopalosiphum* populations fluctuate greatly with local weather conditions in the pastures, as this aphid suffers 90% mor-

tality when exposed to temperatures in excess of 39 °C, whereas the spider populations are not affected by summer temperature extremes. The system has no specialist predators or parasitoids, probably because of the degree to which population numbers of *R. padi* fluctuate during the summer months. During periods of low cereal aphid densities, the spider community, which consists of approximately 11 species, is supported by alternative prey which I suggest comes from detritivores in the soil and litter. The reader should consult Wise et al. (this volume) for further discussion of the topic of external subsidies.

Whatever the mechanism, spiders as agents of biological control can be used in combination with no-till agriculture for the kind of whole ecosystem approach to habitat management that should be encouraged in modern agriculture. While it may be difficult to suggest that a grower decrease pesticide use and apply mulch for its benefits to natural enemies alone, a favorable cost/benefit ratio that might result from these practices in terms of reduced chemical costs; and greater water retention and organic matter accumulation may make the whole ecosystem approach both attractive and practical.

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AFTERWORD

SUMMARY AND FUTURE DIRECTIONS FOR RESEARCH ON SPIDERS IN AGROECOSYSTEMS

Keith D. Sunderland and Matthew H. Greenstone

This symposium, using spiders as a focus, has explored a number of themes of general importance in ecology and biological control. These themes relate to grappling with the problems of scale in the distribution and dispersal of invertebrates, to gaining behavioral insights into the trophic biology of generalist predators, to understanding the functioning of communities and ecosystems, and to launching new initiatives in pest control based on ecosystem engineering. Each of these topics has been illuminated from a range of different angles by the participants, who each approached the symposium with a unique viewpoint and expertise, and the net effect (obtained by reading the full set of Symposium papers) is to provide the reader with a mature and well-rounded appreciation of the subject. The symposium presentations were nothing if not innovative and forward-looking, and they record the forging of some exciting new approaches to the study of ecological processes and the implementation of biocontrol.

Distribution and dispersal: from micro-habitat to landscape.—Individual spiders can move between microhabitats within a habitat by walking. Some of the species characteristic of agricultural systems also have the ability to disperse over short and long distances through the air by ballooning, so they can move between habitats within the landscape during the lifetime of an individual (Samu et al., this volume). Annual recolonization of crops by spiders owes more, in many cases, to aerial deposition of aeronauts than to cursorial invasion from refugia adjacent to fields. The aerial arachnofauna is taxonomically rich, its composition is not representative of ground-based communities, and the size distribution of aeronauts is skewed in favor of small spiders (Suter, this volume). The small size of

aeronauts might not be entirely a result of physical constraints, since a modeling exercise predicted that the optimal dispersal strategy is one of high juvenile dispersal (Topping, this volume). The probability of ballooning can increase in response to a decline in habitat quality, such as crop senescence; and the timing of these changes in habitat quality varies from habitat to habitat within the landscape (Thomas & Jepson, this volume). We have an increasingly detailed understanding of the proximate biological and meteorological constraints and cues for the initiation of aerial dispersal (Suter, this volume), but we know virtually nothing about the fate of aeronauts once they are airborne. Ballooning is risky for the individual. The unpredictable air movement at the time of ballooning could take the individual into danger zones. For the species, however, it is part of the equipment needed for efficient exploitation of the resources offered by ephemeral habitats (Thomas & Jepson, this volume).

To understand why particular strategies of dispersal have evolved it is necessary to consider large spatial areas and long spans of time, and the only practicable way of doing this is through modeling. This aspect of modeling is growing rapidly in sophistication and power (Topping, this volume), but it continues to rely on good-quality biological data. In addition to its contribution to developing ecological theory, landscape modeling could be of practical value if it can produce robust predictions about the optimal patterning of habitats within landscapes, i.e., patterning that will maximize regional populations of natural enemies, including spiders (Samu et al., this volume). Maybe it will also eventually be possible to incorporate a flavor of the topographical, political and economic factors that con-

tribute to the farmer's decision making about the spatial distribution of crop types and other land use decisions.

Prey selection and pest control.—Predation and consumption of pests or alternative foods can be studied in the laboratory, or by direct observation in the field, by gut analytical methods (e.g., radionuclides, electrophoresis, chromatography, serology), or by field experiments (Greenstone, this volume). Laboratory studies are of limited value, serological gut analysis has proved to be the most efficient technique for large-scale studies of the consumption of selected prey species by spiders, and field experiments have demonstrated the value of spiders for biological control. Direct observation has provided good data on dietary range and predation rates in the field (Greenstone, this volume). This method has demonstrated that web-spiders are 99% insectivorous, whereas hunting spiders have a wider diet breadth (Nyffeler, this volume). It is not understood why, despite there being frequent agonistic encounters between web spiders, these rarely result in intra-guild predation (IGP). Many of the hunters, on the other hand are strongly araneophagic (Nyffeler, this volume). Linyphiidae have been found to feed mainly on small Diptera, Homoptera and Colembola, but hunting spiders (Oxyopidae, Thomisidae and Salticidae) eat Diptera, Hymenoptera, Heteroptera, Homoptera, Lepidoptera and Araneae (Nyffeler, this volume).

Some of the factors affecting prey selection have been studied in the laboratory. Active prey selection appears to be a compromise between maximizing energy intake, balancing nutrients and minimizing toxin consumption. Aversions to distasteful, toxic prey (e.g., some aphid species) can be learned by spiders, yet forgotten in less than a day (Toft, this volume). The intriguing possibility has been raised that in some situations pest control might even be improved if the pest is distasteful because of the operation of wasteful killing (= superfluous killing) and unsatisfied spider food demand (Sunderland, this volume). The role of prey quality in determining spider fitness is proving to be a very complex issue. This is a fertile area of current research that is revealing some unexpected facets of the trophic biology of spiders. For example, spiders do not always choose the optimal combination of prey from a mixture, toxic prey in a mixed

diet may inhibit consumption of high quality prey, but if small quantities of other types of toxic prey are consumed they may even improve spider performance (Toft, this volume).

"Limit cycle" control of pests, involving tracking of pest population density by the predator population, is not, generally, a mechanism of pest control that can be attributed to spiders. "Stable equilibrium point or focal control," on the other hand, is a pest control mechanism suitable for spiders and other polyphagous predators that display prey switching and whose populations can be self-limited by cannibalism or territoriality. It relates more to pest control by assemblages of species, rather than to single species of spiders (Riechert, this volume). Spider species often have complementary niches and so an assemblage of species may be able to attack all growth stages of a pest, thus reducing "enemy-free" space and improving the prospects for effective biological control (Sunderland, this volume). Spiders have some additional attributes that increase their value as biocontrol agents. These include a) pest dislodgment, b) the capacity of webs to kill pests even when the spider is absent or unmotivated to attack, and c) wasteful killing and partial consumption (Riechert, this volume; Sunderland, this volume). Whatever the mechanism, solid evidence has accumulated, mainly from field experiments, that spider assemblages can be effective in reducing pest populations and the crop damage that they cause (Greenstone, this volume; Riechert, this volume; Rypstra et al. this volume; Sunderland, this volume; Wise et al., this volume).

Communities and ecosystems.—A major theme here, picked up by various contributors (Riechert, this volume; Sunderland, this volume; Wise et al., this volume) and treated in different ways, is the realization that spiders, as polyphagous predators, can get a subsidy from the detritivore food chain, and that this can boost their impact on herbivores, including pests. It can be argued that ways should be found to apply this principle in agriculture and that there should be research into farming-compatible techniques to increase the detritivore component in a wide range of crops. There could, however, be the penalty that more choice of food may mean that spiders and other generalist predators refuse to eat the pests, especially in cases where the pest spe-

cies are distasteful and toxic (Toft, this volume). Clearly, there is a need for studies directed at determining the outcome of increasing the amount of prey biodiversity in agroecosystems, and at determining the mechanism by which this affects pest control (Wise et al., this volume). There is some evidence that spider predation on detritivores and fungivores can depress rates of litter decomposition and nutrient mineralization in agroecosystems, but this negative effect is expected to be more than offset by the positive effect of spider predation on pests (Wise et al., this volume).

A promising approach to the study of how spider assemblages, as part of a community, affect pest populations, is to see how they fit into functional guilds, rather than always treating them taxonomically. There are indications that this approach is already throwing up some commonalities of community organization that apply across a spectrum of crops (Uetz et al., this volume), but knowledge of the mechanism(s) underlying these findings awaits further research. There is still a dearth of behavioral and life history information for many species, and this is hindering the development of guild classifications and of quantitative comparative guild studies (Uetz et al., this volume). The suggestion that the exact taxonomic composition of these guilds depends heavily on the composition of assemblages in nearby non-agricultural habitats (Uetz et al., this volume) underscores the need for a better understanding of the role of dispersal in the assembly of spider guilds in agro-ecosystems (Samu et al., this volume), especially since the contrary has been observed in experimental garden systems (Riechert, this volume).

A rich complexity of interactions (including various types of competition and intraguild predation (IGP)) can occur between natural enemies in agroecosystems. Some of these interactions are thought to buffer the community from change, while others have been shown to destabilize pest control (Sunderland, this volume; Wise et al., this volume). Both exploitation and interference competition can occur between spider species, especially where preferred microhabitats overlap (Marshall & Rypstra, this volume). Subtle competitive interactions may also be occurring, but investigations of these are still at an early

stage. For example, preliminary results from laboratory mesocosm experiments with two lycosid species suggested that foraging activity of *Pardosa milvina* was reduced in the presence of *Hogna helluo*, even though the two species have contrasting diel activity cycles. A kairomone that alerts *Pardosa* to the presence of a potential predator may be involved (Marshall & Rypstra, this volume). It is hypothesized that complete elimination of a competing species from the crop may be averted if a top predator (such as the strongly araneophagic green lynx spider, *Peucetia viridans*) reduces the density of the dominant competitor (i.e., exploiter-mediated coexistence, as applied to predators) (Sunderland, this volume). Cannibalism and IGP may also enable populations of spiders and other predators to persist in a habitat during periods of low abundance of herbivore and detritivore prey (Marshall & Rypstra, this volume). IGP involving spiders has been studied in natural communities, and IGP involving predators other than spiders has been studied in agroecosystems (sometimes demonstrating that intense predation by one predator on another may release a pest from a former level of satisfactory biological control); but IGP involving spiders in agroecosystems has not yet been investigated experimentally (Hodge, this volume). IGP by lycosid spiders on the insect predators of squash bug eggs was, however, suspected as the explanation for reduced squash production in summer vegetable garden experiments (Wise et al., this volume), and there is a wealth of observational data on the involvement of spiders in IGP relationships in agroecosystems (Nyffeler, this volume). Quantification of density, activity and diet of spiders and co-occurring predators in agroecosystems will enable prediction of the probability of IGP and competition which can then be used to guide the design of rigorous and meaningful field experiments (Hodge, this volume).

Modifications to agricultural practice.—

Ways are being sought to promote the effective use of spiders in biological control; but it should be noted that spiders will, for the foreseeable future, be embedded in integrated management systems which are likely to continue to include some use of pesticides. The selective use of pesticides so that they work with, rather than against, natural enemies

(Riechert, this volume), needs development, and can only be based on a sound understanding of the ecotoxicology of spiders and other natural enemies. Our knowledge of the ecotoxicology of spiders is lagging significantly behind that of some other generalist predators, such as carabid beetles. A strong relationship between spider density and habitat structure has been demonstrated by correlations and experimental manipulations. Measures that increase the structural complexity of the habitat, such as intercropping, mulching and conservation tillage, are known to enhance spider density and diversity (Rypstra et al., this volume). Diversification is most likely to be ef-

fective if it comes in the form of interspersed microhabitats, rather than spatially-segregated microhabitats or habitats (Samu et al., this volume). How the specific details of habitat structure influence the effectiveness of spiders as biological control agents has yet to be worked out. Conservation tillage and mulches are examples of approaches that could simultaneously provide spiders with a more diversified habitat structure and a nutrient and energy boost from the detritivore food chain (Samu et al., this volume; Riechert, this volume; Rypstra et al., this volume; Wise et al., this volume). This topic justifies theoretical, experimental and applied research in the future (Wise et al., this volume).

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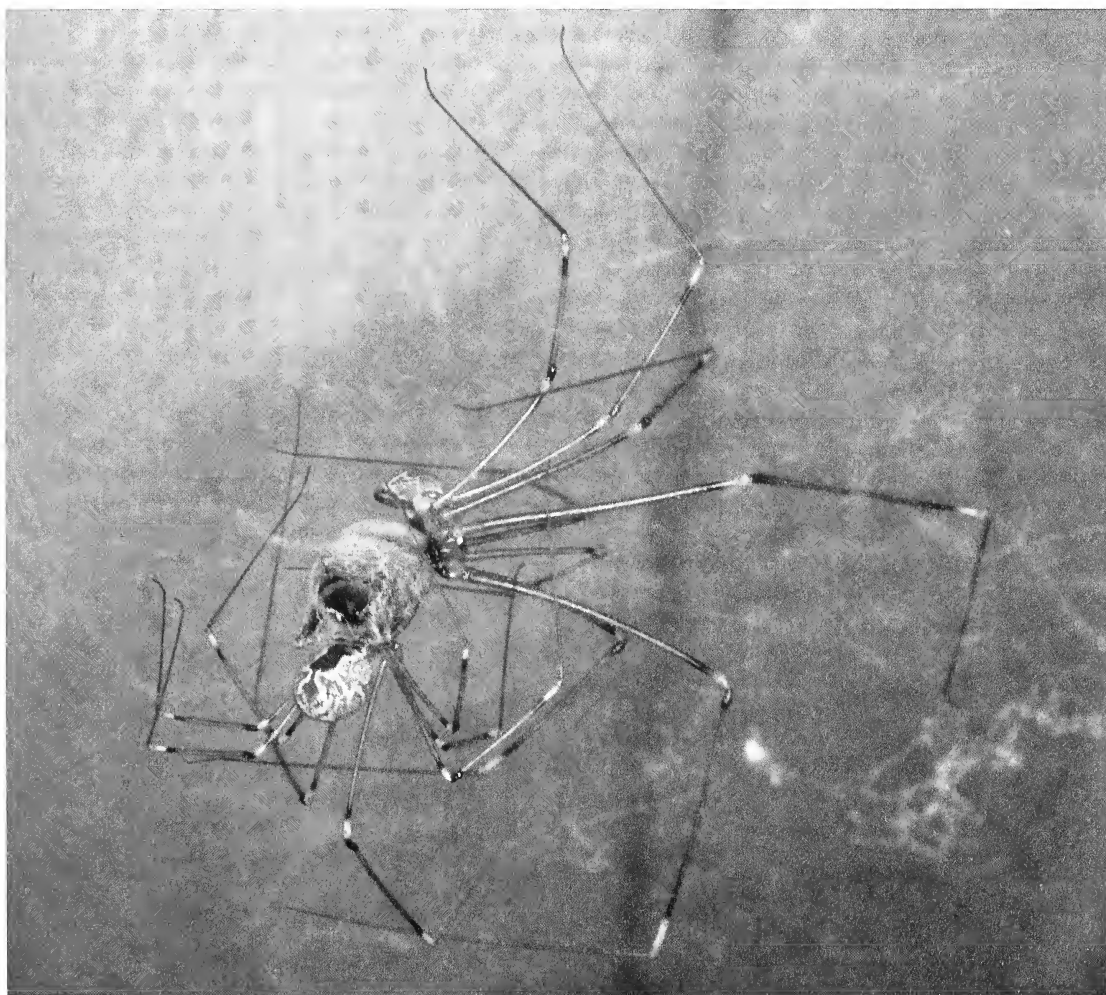
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Cover photo: Two mature female spiders, *Holocnemus pluchei* (Pholcidae), eating a single honey bee, *Apis mellifera*. (Photo by Rick Vetter)

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FOSSIL ARANEOMORPH SPIDERS FROM THE TRIASSIC OF SOUTH AFRICA AND VIRGINIA

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ABSTRACT. New fossil spiders from Triassic rocks of South Africa and Virginia are described. Though lacking synapomorphies of Araneomorphae, certain features suggest they belong in that infraorder, and possibly in the superfamily Araneoidea. Thus, they represent the oldest known fossil araneomorphs and extend the fossil record of the infraorder by approximately 40 Ma to 225 Ma.

Few Mesozoic spiders have been described. Cretaceous mygalomorphs (Eskov & Zonshstein 1990), orbicularian araneomorphs (Selden 1990; Mesquita 1996) and indeterminable Araneae (Jell & Duncan 1986) have been described; and spiders from the Cretaceous Crato Formation of Brazil (Maisey 1991) and Canadian amber (McAlpine & Martin 1963) are currently being studied by PAS. Jurassic records are equally sparse, consisting of a described archaeid (Eskov 1987), the araneoid *Juraranaeus* Eskov 1984, and undescribed filistatids (Eskov 1989). Until now, *Juraranaeus* was the oldest known fossil spider which could be considered an araneomorph. Only one Triassic spider, *Rosamygale* Selden & Gall 1992, has been described: it was placed in Hexathelidae and is the earliest mygalomorph. In this paper, two new fossil spiders are described, both from rocks of Triassic age, thus tripling the number of known Triassic spiders. The specimens show features consistent with Araneomorphae (though synapomorphies of that clade are not preserved), and represent the oldest known fossil araneomorphs. Stratigraphy, paleoecology and locality information is provided for the South African spider by JMA and HMA, and for the Virginia specimen by NCF. All other discussion and systematics are the responsibility of PAS.

METHODS

Terminology and abbreviations.—In the specimens studied, the largest movable cutic-

ular processes are termed bristles; they decline in width from base to tip and in this respect they differ from the spines which occur on many spiders which thicken between base and tip. Smaller and thinner cuticular hairs are termed setae. Abbreviations used in the text and figures: I–IV = first to fourth legs, car = carapace, fe = femur, mt = metatarsus, pa = patella, Pd = pedipalp, st = sternum, ta = tarsus, ti = tibia, trich = trichobothrium. All measurements are in mm.

South African specimens.—The specimen from South Africa (Figs. 2–8) was discovered by JMA and very kindly sent to the senior author by HMA. It originates from the Upper Umkomaas locality in the Triassic Molteno Formation at Natal-Kwazulu, South Africa (Anderson & Anderson 1983, 1984). This is the first fossil spider to be found in South Africa. A second specimen of a possible spider, from the Telemachus Spruit locality in the same formation, was discovered recently; but it is less well-preserved and is not described here.

The Molteno Formation (Fig. 1) was deposited in an extensive, intracontinental foreland basin bounded by rising fold mountains to the south and traversed by a system of braided rivers (Cairncross, Anderson & Anderson 1995). It reaches a maximum thickness of about 600 m and the erosional remnant extends over an area roughly 400 km north to

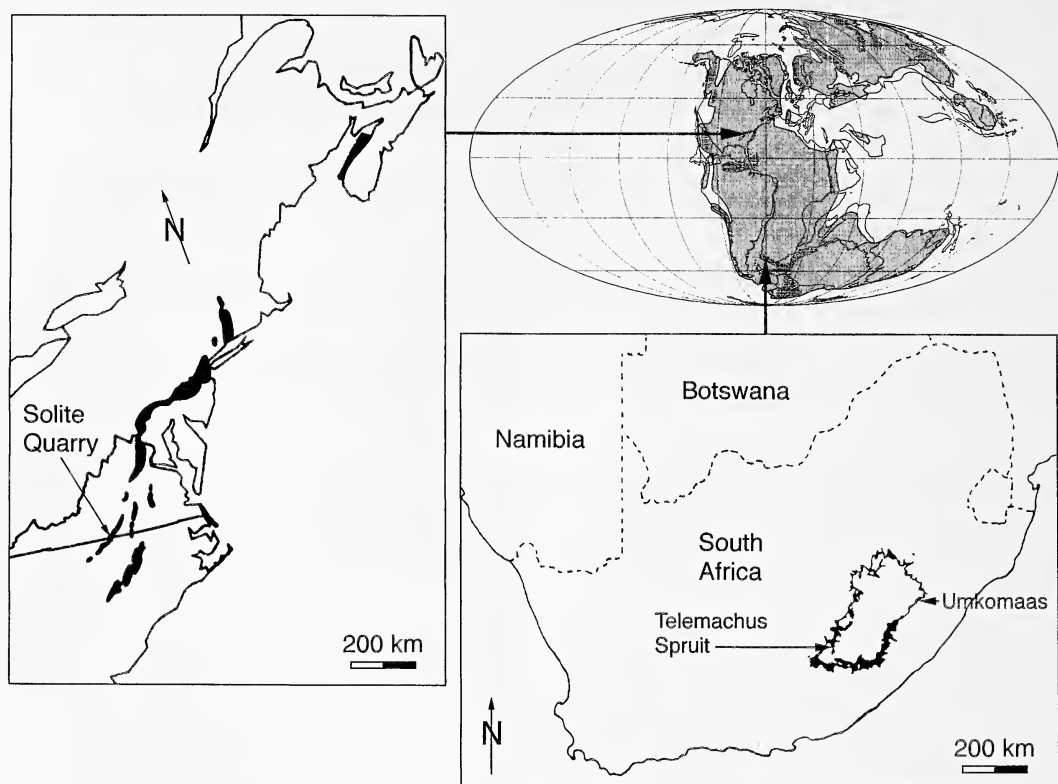


Figure 1.—Location maps of the Solite Quarry, Virginia, in the Danville/Dan River basin (Triassic outcrops shown in black) and localities in the Molteno Formation (shown in black), South Africa, in relation to the late Triassic (~220 Ma) world (land shaded; Triassic outcrops in darker shading). Maps after Anderson et al. 1998; Fraser et al. 1996; Smith et al. 1994.

south and 200 km west to east. The age of the formation is not tightly established, but on the basis of global biostratigraphic correlations (Anderson & Anderson 1983; Anderson et al. 1989) is considered to be Carnian (late Triassic), 222–229 Ma BP. No absolute radiometric ages are available.

A 30-year collecting program (Anderson & Anderson 1983, 1989, 1993a, b; Anderson et al. 1989) has yielded 100 phytotaphocenoses (PTCs, fossil plant assemblages) from the formation. The flora—the richest known globally from the Triassic—includes 56 genera with 204 vegetative species. It is particularly characterized by some 20 species of the seed-fern *Dicroidium* Gothan 1912. There occurs a roughly equal diversity of gymnosperms, including conifers, cycads and ginkgos, along with several new orders, and ‘pteridophytes,’ primarily horsetails and ferns. Though rare, insects comprise by far the most frequently encountered element of the fauna. A remark-

able diversity of 117 genera and 333 species in 18 orders is provisionally recognized in the over 2000 specimens at hand from 43 of the 100 plant assemblages. The beetles, cockroaches and bugs clearly dominate. Conchostraca, from 20 PTCs, are represented by some 3 genera and 8 species. The remaining fauna is sparse: 3 species of fish (impressions only) from 3 PTCs, 2 species of bivalve from 1 PTC, and the 2 spider specimens documented here. Dinosaur trackways, but no skeletal remains, have been identified at a few (non-plant) sites.

The Upper Umkomaas (‘Waterfall’) locality: The fossiliferous bed consists of a dark grey, thinly laminated, carbonaceous shale with excellently preserved plant compressions (with cuticle) and rare insects. Exposed in the bed of a small mountain stream, it reaches 2.3 m in thickness and over 10 m in strike. The shale is interpreted as having accumulated in a non-aerated, abandoned river channel. With

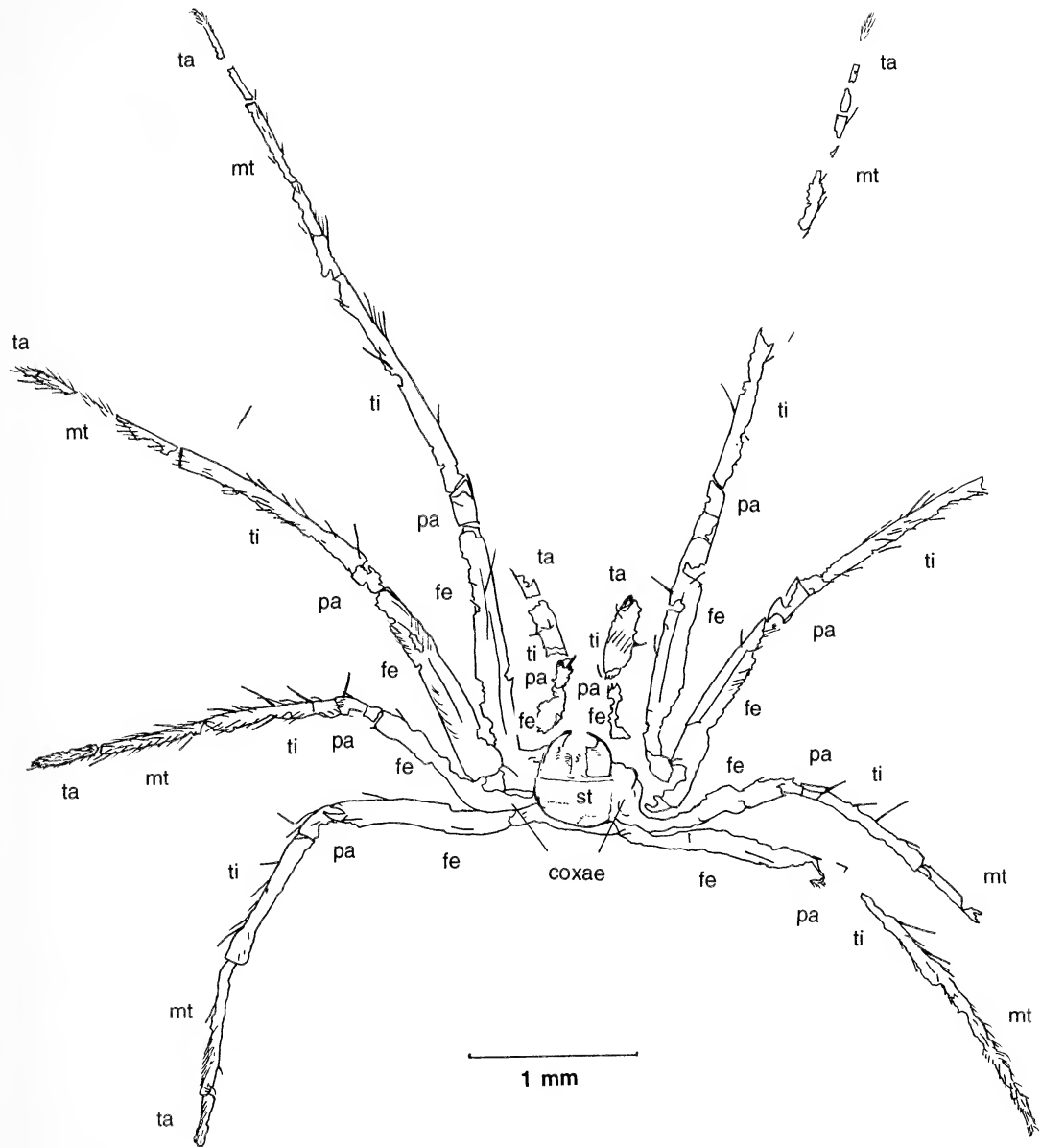


Figure 2.—*Triassaraneus andersonorum* Selden new genus and species, camera lucida drawing of holotype part, PRE/F 18560a, from the Triassic (Carnian) Molteno Formation, South Africa. See Figure 4.

23 genera and 73 species of plant (vegetative taxa), the Umkomaas site has produced by far the richest flora of the 100 Molteno PTCs. The assemblage is seen as representing a dense riverine forest dominated by *Dicroidium*.

The insects from the site, mostly isolated wings and abdomens and—far less commonly—complete adults, now number 166 individuals. The rate of yield is around one specimen per hour when scanning cleaved,

bedding plane surfaces under the microscope. The insect fauna is strongly dominated by cockroaches (80 individuals, 4 species), beetles (63 individuals, 28 species) and bugs (12 individuals, 6 species). The remaining fauna consists of some 70 specimens of Conchostraca in 3 species and the single specimen of spider. The extreme rarity of the spider is clearly emphasized when it is considered that we (JMA & HMA) have to date spent 400

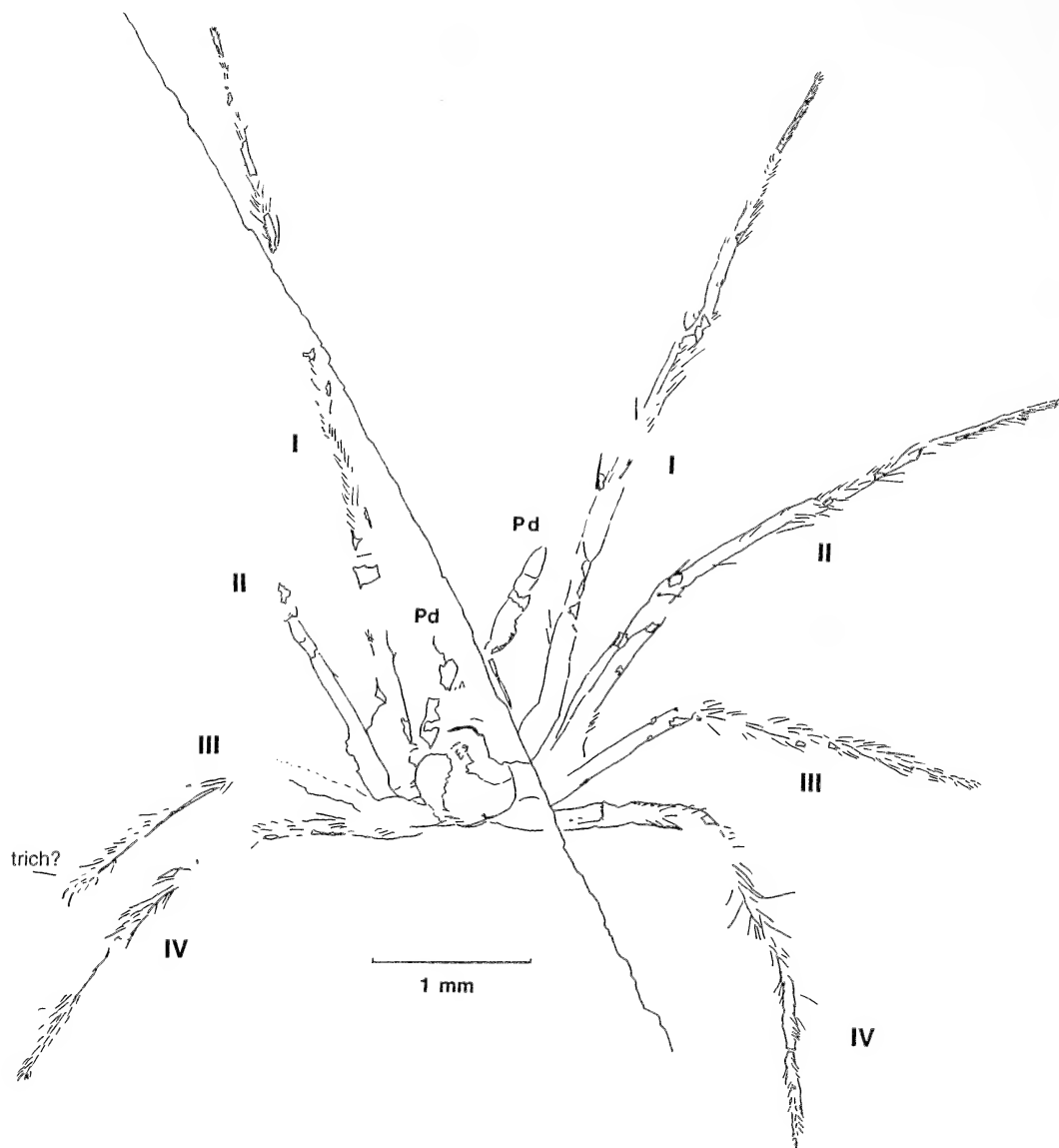


Figure 3.—*Triassaraneus andersonorum* Selden new genus and species, camera lucida drawing of holotype counterpart, PRE/F 18560b, from the Triassic (Carnian) Molteno Formation, South Africa. See Figure 7.

man-hours cleaving plant-fossiliferous slabs from the Umkomaas site, and that the entire curated collection of 2500 cataloged slabs has been carefully scanned under a binocular microscope.

The Telemachus Spruit locality: This site is somewhat different in character from Upper Umkomaas. The plant-fossiliferous bed, a 10 cm thick, buff mudstone, is exposed along a stream bank over approximately 10 m of strike and is interpreted as an abandoned

channel-fill (Cairncross, Anderson & Anderson 1995). The flora (vegetative) of 12 genera and 19 species is strongly dominated by the single coniferous species *Heidiphyllum elongatum* (Morris 1845) Retallack 1981. The assemblage most likely represents two distinct plant communities: a mono-dominant stand of reed-like conifers colonizing sand bars in the braided river and, from farther afield, a *Dicrodium*-dominated riparian forest occupying the river bank. The insect fauna at this site,

represented by only 17 fragmentary specimens, is dominated, as at Umkomaas, by beetles, cockroaches and bugs. The yield remains at around one individual per man-microscope hour. Conchostracans have not been found. The rarity of the single spider specimen is once again emphasized by the fact that JMA & HMA have spent 90 man-hours cleaving slabs at this site and that all 900 curated and cataloged slabs have been carefully scanned for insects or other faunal elements under the binocular microscope.

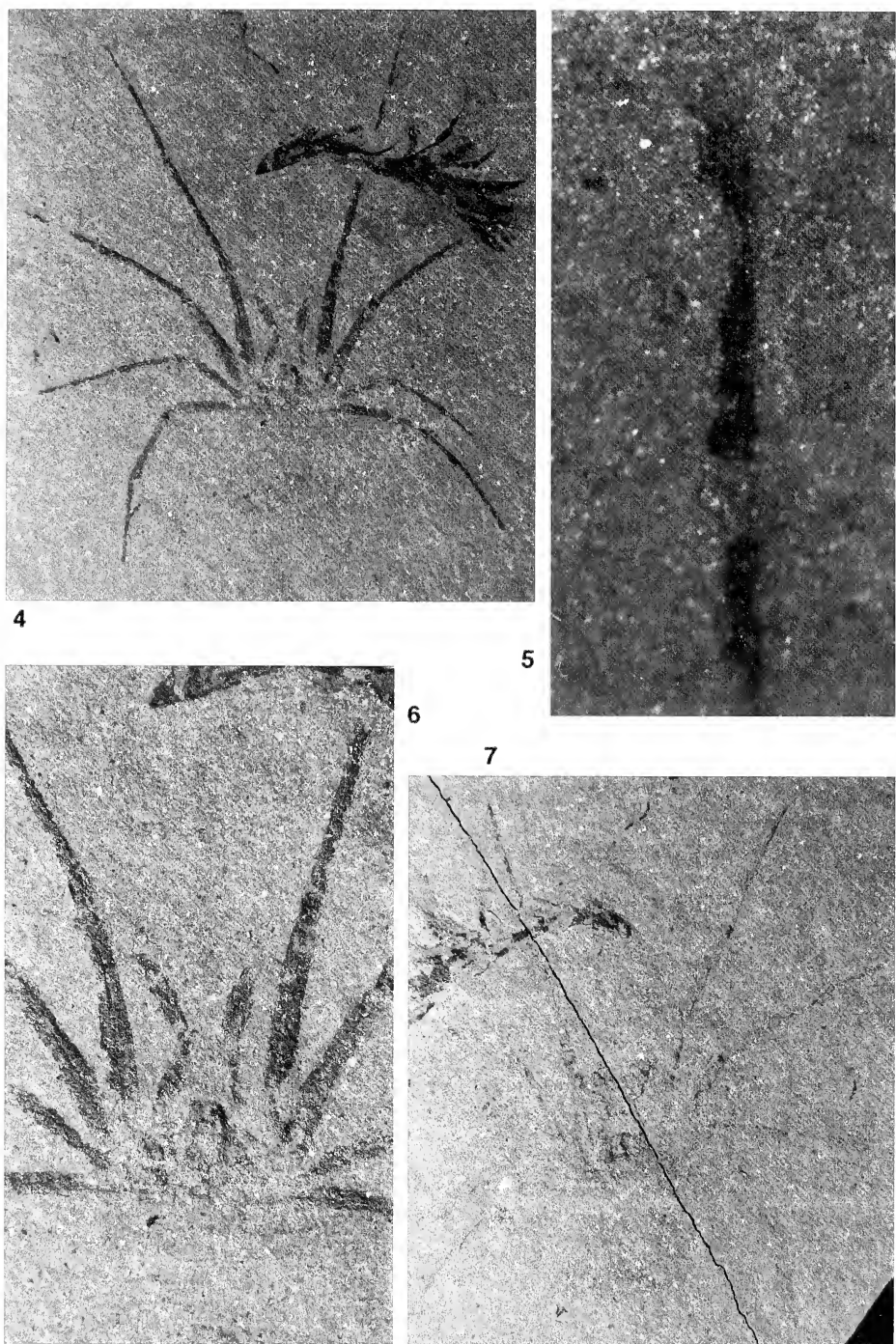
Preservation: The Umkomaas specimen is preserved as brown, organic cuticle on a dark grey shale. Superficially, the cuticle appears black; but under ethanol and high magnification the brown color is evident, and the shale appears paler. The shale is splintery, and pieces readily spall away, necessitating care while studying the fossils. Both part and counterpart eventually cracked after hours of study; the crack on the counterpart is shown in Fig. 7. Scattered throughout the shale are abundant plant remains, including leafy shoots (Fig. 4), spores, and unidentified coalified strands.

The legs are outstretched in a relaxed manner, suggesting that the spider died in the water or was carried there soon after death, thus enabling the muscles to relax. The podomeres are flattened by compression of the shale matrix, but there is a little relief in the form of a pair of oval (long axes sagittal) humps in the anterior half of the prosomal body and a wider oval (long axis transverse) area in the posterior part of the prosomal body. These structures occur on the part with equivalent depressions on the counterpart. Lateral to the prosomal body, the areas representing the coxae, trochanters and basal femora of the legs has a stepped appearance, with each leg overlapping the more posterior leg slightly, and with a sliver of matrix between. The fact of the prosomal humps and the overlapping coxae suggest that the part represents the animal viewed lying on its back, presenting its ventral side to view; the counterpart is mainly an external mold of the ventral surface. The humps on the prosomal body thus represent paired palpal endites with chelicerae beneath (as viewed with the spider on its back) and the sternum behind. The numerous sheets of cuticle, some well-sclerotized, at the anterior end of the prosomal body area, and the convexity of the humps, suggest that the chelicerae as

well as the palpal endites are involved here. The detail of preservation is quite extraordinary, although it has been pointed out (Selden 1989) that the fossilization of a spider is a rare event. When one is recognizable to a collector, it usually turns out to be well-preserved; and the stratum from which it came is dubbed a Fossil-Lagerstätte. Under high magnification, long setae are seen to be abundant on the legs, especially on the more distal podomeres. Larger bristles are apparent, too, as well as the paired claws on some tarsi (Fig. 5), and the details of some joint articulations.

Virginia specimen.—The Virginia specimen (Figs. 9–14) was collected by NCF. It originates from the late Triassic (Carnian) of Virginia and is deposited in the Virginia Museum of Natural History, Martinsville, Virginia. Details of the paleoenvironment and associated fauna are given in Fraser et al. (1996). The early Mesozoic rocks of the Newark Supergroup of eastern North America were deposited in a series of rift basins that formed as Pangaea started to separate (Fig. 1). Collectively, the sediments provide a continuous record from the middle Triassic (Anisian) through to the early Jurassic (Hettangian or younger) (Table 1). The sediments are potentially of enormous value in studies of terrestrial faunal and floral change at this critical period. However, despite their long-time fame for extensive dinosaur trackways (e.g., Hitchcock 1836a, b, 1858; Lull 1915), documentation of other fossils is extremely limited.

The long (167 km), but exceptionally narrow (3–15 km), Danville/Dan River basin in Virginia and North Carolina is one of the more southern basins (Fig. 1). Trackways have been recorded from a variety of localities in this basin (e.g., Fraser & Olsen 1996); and isolated occurrences of tetrapods, fish and plants have also been reported (Olsen & Gore 1989). By far the most significant and productive locality to date is the Virginia Solite Quarry which straddles the Virginia-North Carolina state line. The sediments exposed at the Solite Quarry are referred to the Cow Branch Formation. Paleomagnetic studies indicate that they are equivalent in age to the Lockatong Formation of the Newark basin, most specifically the Nursery through to the Prahls Island members, with the main insect-producing unit probably age-equivalent with the basal Skunk Hollow member (Kent & Ol-



Figures 4–7.—*Triassaraneus andersonorum* Selden new genus and species, holotype from the Triassic (Carnian) Molteno Formation, South Africa; incident light under ethanol. 4. Whole part, PRE/F 18560a; 5. Detail of tarsus and distal metatarsus of left leg I of part showing general preservation and tarsal claws (top), $\times 160$; 6. Detail of body and proximal podomeres of part, $\times 24$; 7. Whole counterpart, PRE/F 18560b, $\times 12$.

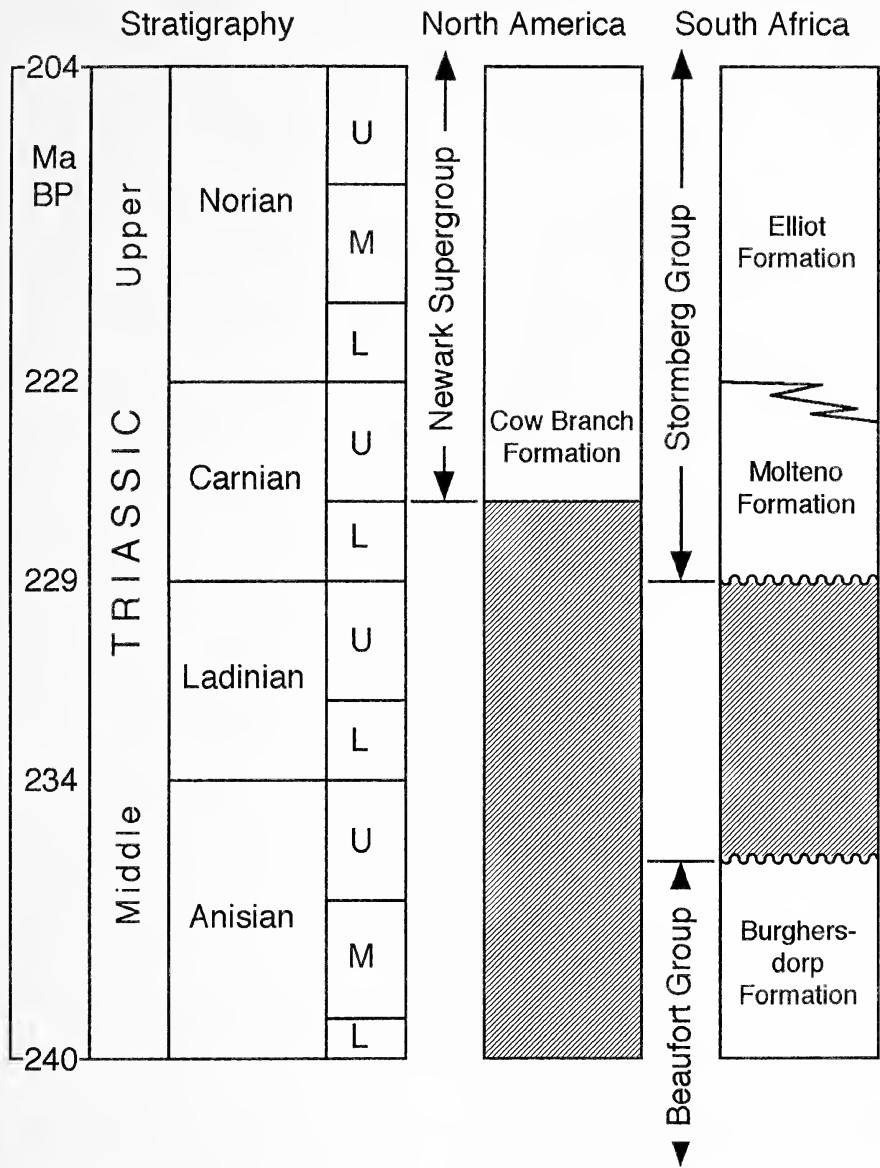


Table 1.—Stratigraphic correlation of the Triassic (Carnian) Cow Branch Formation of Virginia and the Molteno Formation of South Africa.

sen 1997). On this evidence, they are late Carnian in age, which is in close agreement with biostratigraphic studies (Olsen & Gore 1989). Taken together, the three quarries of the Solite Corporation at Cascade expose over 350 m of section. Like other lacustrine rocks of the Newark Supergroup, there is a very clear cyclical pattern of sedimentation which reflects fluctuating lake levels. Typically, each sequence (van Houten cycle) consists of three divisions interpreted as: 1) lake transgression,

followed by 2) a high stand, and then 3) a regression and low stand. These fluctuations are attributed to climate changes which affect the rates of inflow and evaporation (van Houten 1964; Olsen 1986). Each cycle is about 20 m thick. Division 3 facies contain footprints (including *Rhynchosauroides*, *Gwyneddichnium*, as well as those of small theropod and ornithischian dinosaurs), and they also yield root traces and foliage fragments. Division 2 facies are the most fossiliferous. In the upper

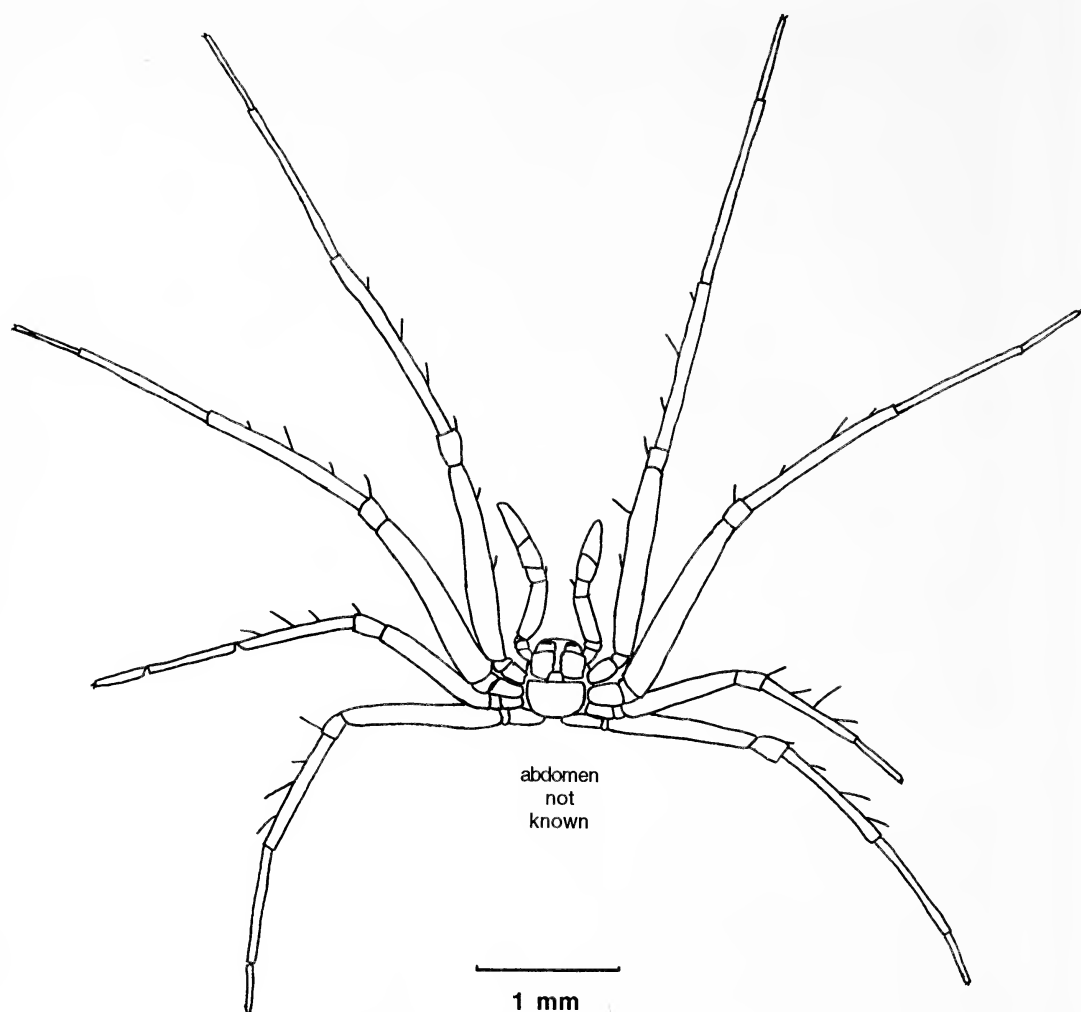


Figure 8.—Reconstruction of *Triassaraneus andersonorum* Selden new genus and species.

portion *Pagiophyllum* and *Brachyphyllum* shoots are common together with cone scales. Towards the base of division 2 diversity levels increase, and there are abundant remains of cycadeoid foliage together with ferns, gymnosperms and occasional ginkgophytes. Vertebrates are also present in these units. Fish are represented by a number of semionotids, redfieldiids, the paleoniscoid *Turseodus* and a coelacanth. The most abundant tetrapod is the prolacertiform *Tanytrachelos*, known from over 200 skeletons. In addition, phytosaurs and a smaller number of other tetrapods are represented by fragmentary remains. The insects occur almost exclusively at the base of division 2. Foliage fragments, particularly of cycadeoids, are fairly common in division 1.

To date, only one area in the quarry has been substantially excavated. In the 1970s, teams from Yale University, under the direction of Paul E. Olson, first realized the potential of the locality and collected over 300 insects from a relatively small (approx. 15 m²) area. This excavation was extended recently by teams from the Virginia Museum of Natural History and Columbia University, but the total area exposed does not exceed 40 m². Most of the time spent in the field is devoted to exposing the fossiliferous units. Once exposed, each man-hour yields, on average, 6 or 7 insects and literally thousands of conchostracans. The cleaved surfaces are scanned in the field using 7× magnification eye visors. The insects are found almost exclusively in two or

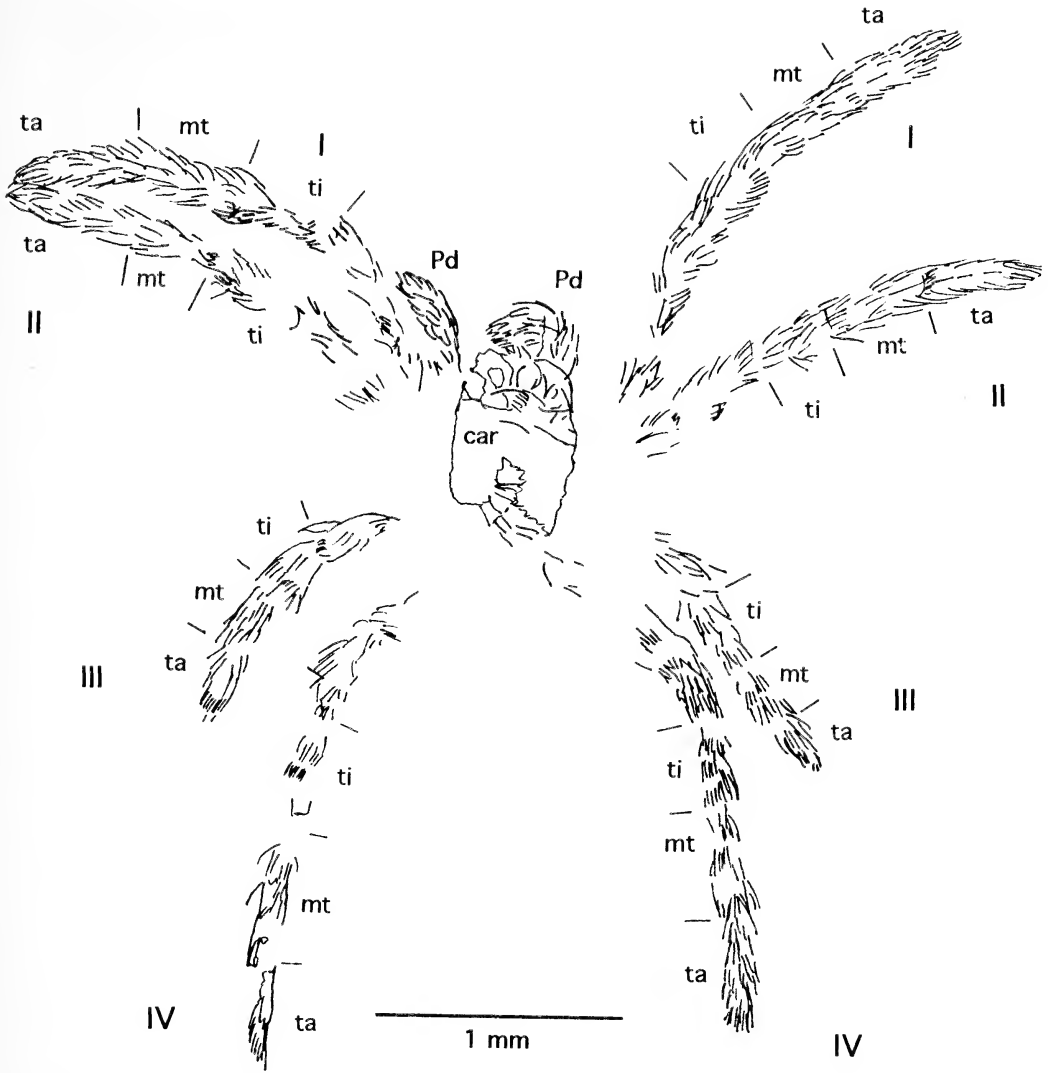
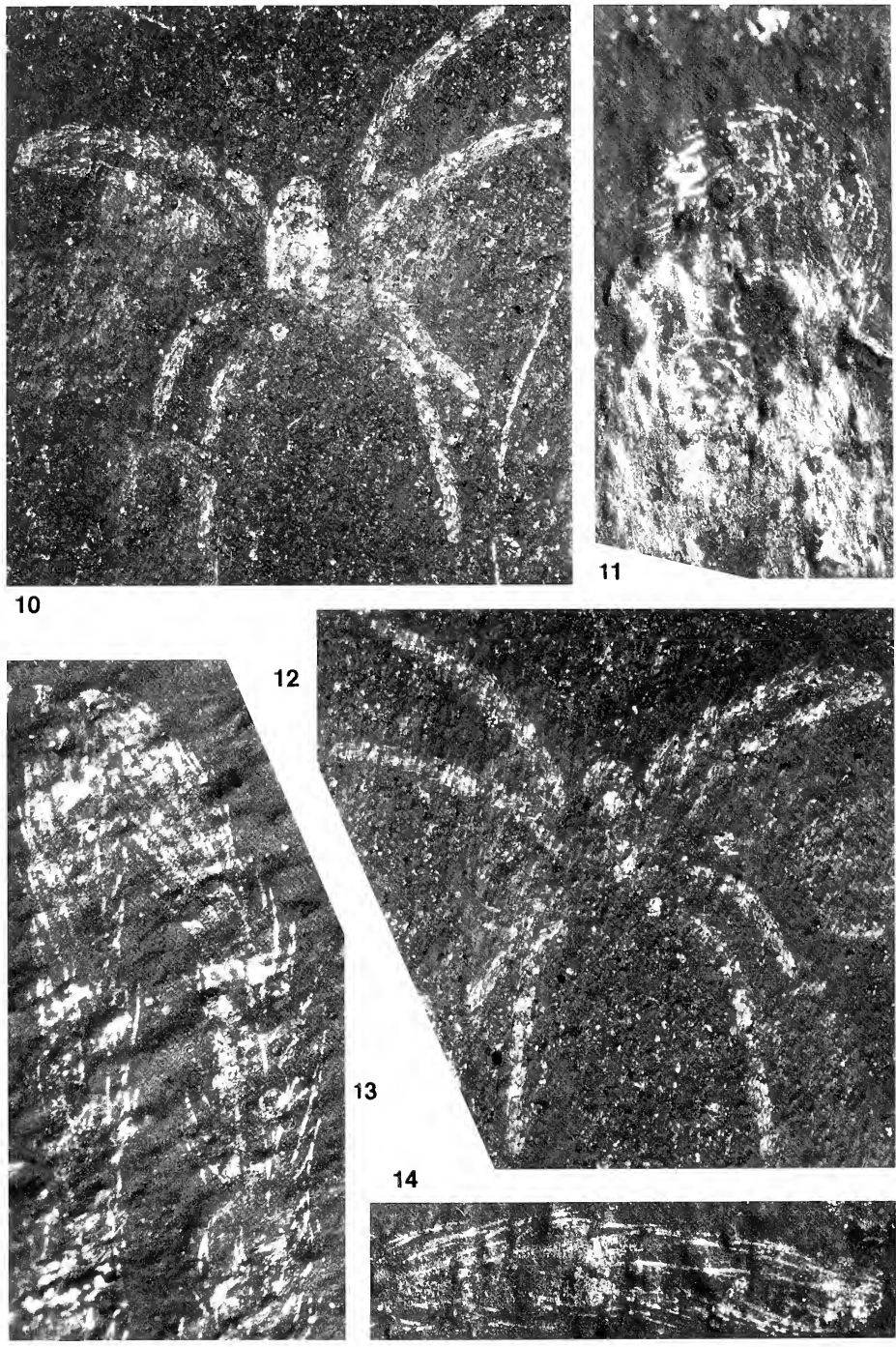


Figure 9.—Camera lucida drawing of *Argyrarachne solitus* Selden new genus and species, holotype, VMNH 782, part, from the Triassic (Carnian), Solite Quarry, Cascade, Virginia. See Figure 10.

three discrete, very thin beds—over 95% of the specimens were uncovered from a single 2.5 cm thick unit. The other units produce abundant plant and vertebrate remains and, while they are unlikely to produce insects, an equal portion of the excavation effort has been channeled towards these units. Some 2500 insects had been collected by mid-1997, when a new insect-bearing unit was identified, containing water bugs in exceptionally high densities (1 cm^{-2}). Thus, the numbers of insects recovered from the Solite quarries is expected to increase. The great majority of the insect finds are of complete individuals. By contrast

with the large number of insects, only two spiders have been recovered, making them a very rare component of the fauna, as they are in the Molteno assemblages.

Preservation: The specimen is almost certainly a juvenile. An additional specimen of a possible spider from the Solite Quarry has been seen by the author, but it is even smaller and less well preserved than the one described here. If it is a spider, then it is also a juvenile. While there is active collecting at the site, hope remains that further, mature specimens might turn up and allow better description of the species.



Figures 10–14.—*Argyrarachne solitus* Selden new genus and species, holotype, VMNH 782, from the Triassic (Carnian), Solite Quarry, Cascade, Virginia; incident light under ethanol. 10. Whole part, $\times 20$; 11. Anterior carapace, palpal endites, chelicerae, and right pedipalp of part, details of endites and chelicerae are obscure. Note matrix bubbles due to mineral growth and patches where silvery cuticle is absent, $\times 85$; 12. Whole counterpart, $\times 20$; 13. Detail of distal parts of left legs I and II of part, note fine preservation of setae, dentate tarsal claws, $\times 100$; 14. Detail of tarsus and distal metatarsus of right leg II of part, $\times 100$.

The specimen is preserved, as are the insects in this deposit, as silver streaks on a black matrix. On the same slab are abundant bivalved crustaceans. The matrix is an extremely fine black shale but contains abundant crystals (gypsum?) which form bubbles on the flat surface of the rock and disrupt the specimen in places (Fig. 11). Finding, studying, and photographing the specimen require considerable manipulation of the light source and the use of ethanol to enhance the contrast between silvery streaks and matrix. Nevertheless, very fine details, such as leg setae, can be seen. The carapace and pedipalp endites are preserved as sheets of silvery cuticle. The absence of patches of cuticle in the anterior carapace region gives the appearance of large eyes, but higher magnification (Fig. 11) shows this not to be the case. Patches where cuticle is absent on the part (Fig. 10) can be matched with the presence of cuticle on the counterpart (Fig. 12). The carapace is approximately rectangular; its anterior border is obscured by presumed chelicerae and palpal endites. The pedipalps are preserved bent to the left in the part. The walking legs are setose but lack bristles or spines, and the proximal podomeres are poorly preserved. The tarsal claws are small and stout, and small teeth can be seen in Figs. 13 and 14. Leg III is very short; and legs I, II, and IV are approximately the same length, giving a leg formula of 1243. The abdomen is not preserved. The specimen almost certainly represents a juvenile, as evidenced by the short, undifferentiated podomeres. Presumably, like the South African specimen, it fell into the lake waters and died there.

DISCUSSION

There is little doubt that the South African specimen is a spider; no other arachnid order presents the same arrangement of prosomal appendages, palpal endites and sternum. The broad sternum and presence of palpal endites (not known in mesotheles and most mygalomorphs) precludes the fossil from Mesothelae. If the spider were a mesothele or a mygalomorph, then the orthognath chelicerae would be expected to protrude conspicuously well beyond the front of the body, as they do in compression fossil mesotheles (Selden 1996) and mygalomorphs (Eskov & Zonshtein 1990; Selden & Gall 1992) but not araneomorphs except where specially enlarged, e.g., in some

adult males (Eskov 1984; Selden 1990). Rather, the most anterior fragments of chelicerae occur only just anterior to the humps which represent the cheliceral bodies and palpal endites. The general appearance of the spider, with rather long and slender legs, a leg formula of 1243, lack of leg scopulae and with generally rather sparse bristles, are features suggestive of Araneomorphae rather than Mygalomorphae. Furthermore, this leg shape and arrangement, the lack of spines (only bristles), the small tarsal claws and lack of scopulae, the paucity and arrangement of bristles, and the possible metatarsal trichobothrium seen on one leg are all suggestive of Araneoidea. While it is impossible to be precise about the number of leg bristles, there appears to be a pattern. All legs have a superior bristle near the distal edge of the patella (also on the pedipalp) and a row of three bristles on the superior side of the tibia. In addition, there are at least two bristles on the superior side of femur I. Griswold et al. (1998) demonstrated the existence of a clade of Araneoidea in which femoral spination is lacking—the spineless femora clade—which includes Theridiidae, Nesticidae, Cyatholipidae and Synotaxidae. The South African fossil spider cannot belong in this clade.

Circumstantial evidence may also be helpful in determining the systematic placement of the South African spider. The Molteno shale is interpreted as having accumulated in an anaerobic, abandoned river channel. Many modern spiders live close to such an environment, including lycosoids (e.g., lycosids and pisaurids) which favor damp habitats, and tetragrathids which build orb webs among waterside vegetation. Lycosoids are adept at walking on water, but orb-weavers are likely to drown if they actually fall into water. Indeed, a fossil tetragrathid and other orb-weavers are known from waterside situations in the Jurassic and Cretaceous (Eskov 1984; Selden 1990). The preservation of the Triassic mygalomorph, *Rosamygale* Selden & Gall 1992, was unusual in that sea-water inundation was involved.

The identity of the Virginia specimen is less secure. Like the South African specimen, it is also clearly a spider because of the leg and podomere arrangement. The short, undifferentiated podomeres and undeveloped pedipalp suggest an immature. The very short third leg

is distinctive and typical (but not diagnostic) of Orbiculariae. The short, dentate tarsal claws do not give a clue to relationships but are common among web weavers.

In the *Treatise on Invertebrate Paleontology*, Petrunkevitch (1955) listed five genera of spiders from the Carboniferous period tentatively referred to Araneomorphae. Three of these, *Archaeometa* Pocock 1911, *Arachnometa* Petrunkevitch 1949, and *Eopholcus* Frič 1904 (family Archaeometidae Petrunkevitch 1949) were placed in a new superfamily Archaeometoidea Petrunkevitch 1955, diagnosed as 'Presumptive Trionychi with segmented abdomen.' The other two, *Pyritaranea* Frič 1901 and *Dinopilio* Frič 1904 (family Pyritaraneidae Petrunkevitch 1953), were placed in a new superfamily Pyritaraneoidea Petrunkevitch 1955 and diagnosed as 'Presumptive Dionychi with laterigrade legs and segmented abdomen.' Petrunkevitch (1955: 132) noted problems in regarding these specimens as araneomorphs: abdominal segmentation and lack of araneomorph synapomorphies. All of these specimens are currently being studied by PAS. Preliminary studies indicate that *Archaeometa*, *Arachnometa*, and *Dinopilio* are arachnids but not spiders, while *Eopholcus* and *Pyritaranea* may be spiders but are not sufficiently well preserved to determine their affinities. No other fossil araneomorph spiders are known from the Paleozoic era or the Triassic period of the Mesozoic era, thus the specimens described herein are the oldest known fossil spiders which can be referred to Araneomorphae with some degree of confidence.

The discovery of araneomorph spiders in the Triassic period is not unexpected, since the existence of their sister group, Mygalomorphae, in strata of similar age (Selden & Gall 1992) predicts this. Furthermore, the discovery of a mesothel spider in rocks of Pennsylvanian age (Selden 1996) is a predictor that Opisthothelae (Mygalomorphae + Araneomorphae) occurred at that time too, so it is indeed possible that araneomorph spiders may be found in earlier strata. However, no fossil spiders have yet been found in strata of Permian age (which immediately precedes the Triassic), despite the fact that a vast number of insect fossils are known from that period. Fossil spiders from this period should prove to be extremely interesting (Eskov 1990). The fos-

sils described here are not primitive araneomorphs, which suggests that a fair degree of radiation had occurred among araneomorphs before the late Triassic. The existence of similar forms in South Africa and Virginia, widely separated geographically and subject to different climatic regimes (though on the same continent), is further evidence in support of this hypothesis.

SYSTEMATICS

[*Note:* Due to the lack of autapomorphic characters, the diagnoses given below are not comparative.]

Infraorder Araneomorphae Smith 1902
?Superfamily Araneoidea Latreille 1806
Triassaraneus Selden new genus

Type and only species.—*Triassaraneus andersonorum* new species, see below.

Etymology.—The genus name refers to Triassic, the stratigraphic period from which the specimen originates, and *Araneus*, a widespread genus of spiders which the fossil superficially resembles.

Diagnosis.—Araneomorph spider, possibly araneoid; sternum wider than long and with straight anterior border.

Triassaraneus andersonorum Selden new species
Figs. 2–8

Holotype.—PRE/F 18560a (part) and 18560b (counterpart), immature, or mature female, from Member Z of the late Triassic (Carnian) Molteno Formation at the Upper Umkomaas 'Waterfall Locality' (UMK III), Natal-Kwazulu, South Africa; deposited in the National Botanical Institute, Pretoria, South Africa.

Etymology.—The trivial name honors Drs. John and Heidi Anderson who found this specimen and kindly passed it on for description.

Diagnosis.—As for the genus.

Description.—Carapace not visible. Anterior part of prosomal body shows a pair of humps representing palpal endites and chelicerae beneath (as specimen is viewed). Layers of cuticle bearing well-sclerotized areas also suggest this is the case. Posterior to palpal endites another raised area represents sternum which is wider than long, posterior border gently procurved, anterior border straight, lat-

eral edges more vague but apparently curved outwards. Pedipalp fe, pa and ti/ta preserved, latter podomeres rather thickened, and visible on left side of part extending beyond cuticle fragment as a hump (*cf.* endites and chelicerae); pa bears superior bristle. Approximate lengths of Pd podomeres: fe 0.3, pa 0.1, ti/ta 0.4. All legs with superodistal bristle on pa, line of 3 superior bristles on ti (middle longest), small paired ta claws (median claw not seen), no scopulae; possible mt trichobothrium visible on leg 3, leg I fe with row of at least 2 superior bristles. Approximate lengths of leg podomeres: leg I: fe 1.3, pa 0.2, ti 1.4, mt 1.2, ta 0.6, total 4.7; leg II: fe 1.3, pa 0.2, ti 1.2, mt 1.0, ta 0.3, total 4.0; leg III: fe 0.9, pa 0.2, ti 0.8, mt 0.7, ta 0.4, total 3.0; leg IV: fe 1.0, pa 0.2, ti 0.9, mt 0.8, ta 0.3, total 3.2. Leg formula 1243. Abdomen not visible.

Argyrarachne Selden new genus

Type and only species.—*Argyrarachne solitus* new species, see below.

Etymology.—Greek: *argyros*, silver, and *arachne*, a spider, referring to the appearance of the fossil spider as silvery streaks on a black rock.

Diagnosis.—Araneomorph spider with subrectangular carapace and short, stout, dentate tarsal claws.

Argyrarachne solitus Selden new species Figs. 9–14

Holotype.—VMNH 782 (part and counterpart), immature, from the late Triassic (Carnian) Cow Branch Formation at Solite Quarry, Cascade, Virginia; deposited in the Virginia Museum of Natural History, Martinsville, Virginia.

Etymology.—The trivial name refers to the Virginia Solite Corporation, in whose quarry the specimen was found.

Diagnosis.—As for the genus.

Description.—Carapace roughly parallel-sided with straight posterior margin, anterior border obscured by presumed chelicerae and palpal endites. Total length of preserved carapace + chelicerae/endites 0.7 mm. Pedipalps short, not swollen. Walking legs setose, lacking bristles, proximal podomeres poorly preserved. Tarsal claws small, stout, dentate. Approximate lengths of leg podomeres: leg I: ti 0.42, mt 0.43, ta 0.51; leg II: ti 0.38, mt 0.39, ta 0.51; leg III: ti 0.31, mt 0.29, ta 0.26; leg

IV: ti 0.43, mt 0.49, ta 0.45. Leg III very short, legs I, II, and IV approximately the same length; leg formula 1243. Abdomen not preserved.

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NEW SPECIES AND CLADISTIC REANALYSIS OF THE SPIDER GENUS *MONAPIA* (ARANEAE, ANYPHAENIDAE, AMAUROBIOIDINAE)

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ABSTRACT. The known range of the South American genus *Monapia*, previously known only from temperate South American forests, is expanded to central and eastern Argentina and Uruguay. A monophyletic group of five species with spinose forelegs is proposed, including *M. angusta*, newly transferred from *Arachosia*, plus four new species: *M. charrua*, *M. guenoana*, *M. fierro* and *M. carolina*. One new species, *M. tandil* (from Buenos Aires Province), is proposed to be the sister group of *Monapia vittata*. A data matrix with 43 characters for the 13 species of the genus (plus 9 amaurobioidine outgroups) was cladistically analyzed. Although relationships among species are mostly resolved, the basal phylogeny of the genus remains unclear. The previous hypothesis of relationships of *Monapia alupuran* is unsupported in this new analysis. Additional records are given for *M. lutea* and *M. dilaticollis*.

The genus *Monapia* Simon 1897 was revised in a recent contribution (Ramírez 1995b). The seven species there included are endemic of the temperate forests of Southern Chile and adjacent Argentina. Mello-Leitão (1944) described *Arachosia angusta* from Buenos Aires, Argentina, a very peculiar species with elongate body, flat carapace and remarkably spinose forelegs. In recent years, two very similar undescribed species were collected on large riparian grasses from Buenos Aires and adjacent regions, and because of the highly modified body and bizarre leg spination they were thought to belong, together with *Arachosia angusta*, to a separate, undescribed genus. However, a reexamination of genitalic characters in *Arachosia angusta* and those two related species showed a depressed median area on the epigynum, a character previously considered as synapomorphic of *Monapia* (Ramírez 1995b), and the divided male conductor typical of that genus (i.e., Fig. 11). These species have extremely cryptic habits. Their elongate body helps camouflage the spiders on grass leaves, while the yellowish and spotted coloration mimics that of the dry leaves. *Monapia guenoana* new species females were found covering their eggsacs with their own body; and even when exposed to view, they were discerned with difficulty.

Besides these three elongate and very spinose spiders, I consider two more new species collected in grasslands of central Argentina. They also have spinose fore tibiae, but a typical amaurobioidine appearance. As shown below, these five species form a monophyletic group distributed in a region generically known as Pampas, where the main plant communities are grasslands. Finally, I include one new species close to *Monapia vittata* (Simon 1884) which was previously considered the sister group of all other species of the genus. In the light of these additional taxa and several new characters, a cladistic reanalysis for all *Monapia* species was undertaken. This analysis challenges some of the conclusions of my previous revision.

METHODS

The format of the descriptions follows Ramírez (1995b). Spermathecae for scanning microscopy were treated as in Sierwald (1990). All measurements are expressed in millimeters.

Specimens are deposited in the following institutions: CAS = California Academy of Sciences (Charles Griswold); IRSN = Institut Royal des Sciences Naturelles de Belgique, Brussels (Louis Baert); MACN = Museo Argentino de Ciencias Naturales “Bernardino

Rivadavia," Buenos Aires (Cristina Scioscia); MLP = Museo de La Plata (Carola Sutton de Licitra, Luis Pereira); ZMK = Zoologisk Museum, Copenhagen (Henrik Enghoff).

CLADISTIC ANALYSIS

All characters considered in a previous revision (Ramírez 1995b) were taken into account. Some descriptive terminology was modified as in Ramírez (1995a). Multistate characters were considered additive when the states are interpreted as internested homologies. This is not intended to express any assumption on the evolution of characters, but merely reflect degrees of similarity (Lipscomb 1992; Goloboff 1997). Morphoclines were interpreted as internested homologies. Because this approach might be suspected by some authors as an unjustified assumption, additional runnings were made with all characters non-additive. This analysis produced identical trees and statistics, thus demonstrating that the obtained phylogeny does not depend on my interpretation of morphoclines. The root of the tree was placed according to the subfamilial analysis made in Ramírez (1995a). Anyphaeninae was used as a more distant outgroup. Because the relationships among the 32 genera of that subfamily are unknown (Brescovit 1997), most entries were coded as polymorphisms, according to the variability found throughout genera. The resolution of the outgroups changed slightly from the previous analysis of the genus (Ramírez 1995b), according to new knowledge of the genera related to *Amaurobioides* Hickman 1949 (Ramírez 1997).

Character 0: Body pattern, 0 = dark patches or uniform, 1 = dark spots on light background (Fig. 1). Character 1: Carapace outline, 0 = oval (Fig. 35), 1 = lengthened (Fig. 8). Character 2: Carapace height, 0 = normal, the posterior slope begins near the thoracic fovea (Fig. 24), 1 = flattened, the slope begins well behind the thoracic fovea (Figs. 7, 14). Character 3: Posterior eye row, 0 = procurved or straight, 1 = recurved. Character 4: Abdomen shape, 0 = oval, 1 = lengthened. Character 5: Number of retromarginal cheliceral teeth, 0 = two, 1 = three, 2 = four or more. The character is considered additive (corrected additivity from Ramírez 1995b). Character 6: Long ventral hairs on male palpal tibia, 0 = absent, 1 = present. Re-examined from Ra-

mírez (1995b) and scored as absent in *Monapia alupuran* Ramírez 1995 because the hairs in *M. alupuran* are shorter than those on *M. vittata*, and very similar to those in other *Monapia*. Character 7: Cymbial basal retro-lateral notch, 0 = absent, 1 = weak (Figs. 27, 36), 2 = strong (Ramírez 1995b: fig. 48). Some undescribed species that probably belong to *Oxysoma* Nicolet 1849 have a strong cymbial notch. Considered additive. Character 8: Tegulum with a deep notch occupied by the median haematodocha, 0 = absent, 1 = present. Character 9: Trajectory of sperm duct, 0 = parallel to tegular notch, 1 = with a curve near the apical margin of tegulum. Coding and internal step for *Oxysoma* as in Ramírez (1995b: character 8). Character 10: Shape of paramedian apophysis, 0 = thick, 1 = thin, 2 = long and very thin. Considered additive. Character 11: Amaurobioidine paramedian apophysis closely associated with median apophysis (Ramírez 1995a), 0 = absent, 1 = present. Character 12: Length of basal portion of embolus, 0 = short, 1 = very long. The intermediate state "long" considered in Ramírez (1995b) is here ignored because after the addition of new species the distinction between "short" and "long" is equivocal. Character 13: Shape of basal portion of embolus, 0 = cylindrical, 1 = flattened. Character 14: Extension of basal embolar unsclerotized area, 0 = absent or small, 1 = wide. The scoring of "small" as an intermediate state made in the previous revision is not used here because it is scored in character 12 state 1 (the basal portion of the embolus is defined by the presence of the unsclerotized area). The wide and folded unsclerotized membrane present in *M. lutea* (Nicolet 1849) and *M. huaria* Ramírez 1995 is instead very different from the basic pattern of embolar morphology. Character 15: Grooved primary conductor (Ramírez 1995a), 0 = absent, 1 = present. Character 16: Secondary conductor, 0 = present, 1 = absent. Character 17: Groove in secondary conductor, 0 = absent (Figs. 38–39), 1 = present. In most *Monapia* species the secondary conductor is divided by an unsclerotized area, and the groove remains on the prolateral portion. Character 18: Division of secondary conductor (Ramírez 1995b), 0 = entire, 1 = divided by an unsclerotized area (Fig. 11). Character 19: Unsclerotized area of secondary conductor with a lobe, 0 = absent, 1 = present. Char-

acter 20: Prolateral portion of the secondary conductor displaced towards the base of the embolus, 0 = apical, 1 = displaced (Figs. 37, 39). Character 21: Denticles on prolateral portion of the secondary conductor, 0 = absent, 1 = present (Fig. 37). Character 22: Retrolateral portion of the secondary conductor fused to tegulum, 0 = free (Fig. 16), 1 = fused (Fig. 10). Character 23: Denticles on retrolateral portion of secondary conductor, 0 = absent, 1 = present. Character 24: Shape of base of retrolateral portion of secondary conductor, 0 = thick, 1 = thin and wide. Character 25: Anterior pouch on median epigynal field, 0 = absent, 1 = present (Fig. 4). Character 26: Shape of epigynal anterior pouch, 0 = pit like (Fig. 13), 1 = transversal furrow (Fig. 19). *Monapia angusta* is scored as uncertain because the opening is circular but prolonged to the sides in a furrow between the median field and lateral lobes. Character 27: Cavities on epigynal anterior pouch, 0 = a single pit or furrow, 1 = two cavities (Figs. 5, 30). Character 28: Central depression on epigynal median field, 0 = absent, 1 = present (Fig. 4), 2 = vestigial. Polymorphic entries and non-additivity justified in Ramírez (1995b). Character 29: Median pouch on epigynal median field, 0 = absent, 1 = present (Fig. 12). Variable through individuals of *M. dilaticollis* (Nicolet 1849) (see Ramírez 1995b: figs. 35–39). The small foldings found on *M. angusta* (Fig. 22) and *M. fierro* new species (Fig. 4) might be homologous to the median pouch; the character is coded as uncertain for these species. Character 30: Position of epigynal lateral lobes, 0 = separate, 1 = contiguous, 2 = fused with a median suture, 3 = fused without suture. Considered additive. Character 31: Degree of fusion of proximal copulatory ducts, 0 = separate, 1 = fused with median wall, 2 = totally fused with common lumen. Considered additive. The “unpaired copulatory duct” considered in the previous analysis as an independent character is subsumed here in the state 2. Character 32: Copulatory plug in mated females, 0 = absent, 1 = present. *M. angusta* was coded uncertain because only one female is known, which lacks plug. Entries coded as absent are based on numerous specimens. Character 33: Shape of spermathecae, 0 = irregular, 1 = spherical or oval. Character 34: Shape of copulatory ducts, 0 = thick, outline of duct not well distinct from that of

spermatheca, 1 = thin at least on distal portion, well distinct from outline of spermatheca. Character 35: Shape of anterior copulatory ducts, 0 = narrow (Figs. 19, 34), 1 = wide (Ramírez 1995b: figs. 61, 79). Character 36: Thickness of walls of proximal copulatory ducts, 0 = thick, 1 = thin. Character 37: Length of female tibia + metatarsus III, 0 = longer than tibia IV, 1 = shorter than tibia IV, 2 = shorter than 75% of tibia IV. Considered additive. Character 38: One strong anterior spine on chelicerae, 0 = absent, 1 = present. Scored as polymorphic in *Oxysoma*, because the spines are absent in *Oxysoma valdiviensis* (Simon 1897) but present in some undescribed species. Character 39: Ventral spines on female palp, 0 = absent, 1 = present. Character 40: Prolateral/ventral spines on anterior femora, 0 = absent, 1 = one (Figs. 24, 32), 2 = several. *M. charrua* new species and *M. angusta* have an oblique line of thick setae (Figs. 7, 20) in similar position as the thick spines of *M. guenoana* (Fig. 14), with which are presumed to be homologous. Considered additive. Character 41: Number of ventral spines on anterior tibiae, 0 = three pairs or less, 1 = four pairs or more. Character 42: Thickness of ventral spines on anterior tibiae, 0 = normal, slender (Figs. 24, 32), 1 = strong (Figs. 7, 14, 20). Character 43: Apical ventral spines on anterior tibiae, 0 = present, 1 = absent.

The data matrix of Table 1 was analyzed under parsimony using implied weights (Goloboff 1993, 1995), using Pee-Wee version 2.5.1 (Goloboff 1996a). This program assigns lower weight to characters showing more homoplasy. Internal steps of characters were assigned as implied by polymorphic terminals with command *ccode* =. Polymorphisms in Anyphaeninae were not taken into account for this purpose, because in such large group most characters are polymorphic, and it seems improper to decrease the weight of characters because of variability in a group so distant.

A heuristic search of 100 independent Wagner trees, each followed by TBR branch swapping (command *mult*100*;) produced the same two trees in all replications, for any value of the constant of concavity K ($1 \leq K \leq 6$). A strict consensus of the two trees is shown in Fig. 6. The cladograms have a length of 79 steps, consistency index (for informative characters only) of 0.65, a retention index of 0.83, a fit (sum of implied weights)

Table 1.—Data matrix for *Monapia* species and outgroups. x = [01], y = [012], z = [02], ? = unknown, - = uncertain. Commands for additivity and internal steps: ccode = 7 9 29 38 * = 1 9 *- , + 5 7 10 30 31 37 40;.

	1			2			3			4		
	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	0123	0123
<i>Anypaeninae</i>	0000x	2000-	--XXX	00-0-	-----	xxxx-	x0x0x	xy000	xxxx	xy000	xxxx	xxxx
<i>Coptoprepes</i>	00000	20010	--000	11-0-	---00	0--00	00000	00000	0000	00000	0000	0000
<i>Anaurobioides</i>	00010	10010	--000	11-0-	---00	0--00	00000	00000	0000	00000	0000	0000
<i>Ferrieria</i>	00010	20010	00000	1110-	00100	0--00	00000	00000	0110	00000	0110	0110
<i>Arachosia</i>	00000	00010	11000	0110-	00000	11?00	00011	00000	0000	00000	0000	0000
<i>Sanogasta</i>	00000	00010	11000	0110-	00000	1000?	?0011	00000	0000	00000	0000	0000
<i>Gayenna</i>	00000	00010	00000	0110-	000x0	10000	00011	00000	0000	00000	0000	0000
<i>Liparotoma</i>	00000	00010	00000	0110-	00000	10000	00011	00000	0001	00000	0001	0001
<i>Oxysoma</i>	10101	00z11	00000	0110-	100x0	10000	00011	000x0	0000	00000	0000	0000
<i>Tasata</i>	10000	20011	00000	0110-	100x0	10000	00011	00000	0000	00000	0000	0000
<i>Monapia vittata</i>	10000	01211	00000	01010	11000	11010	00111	00000	0000	00000	0000	0000
<i>Monapia alupuran</i>	10000	00011	10000	01111	10000	11110	00111	00000	0000	00000	0000	0000
<i>Monapia dilaticollis</i>	10000	00011	10010	01111	00111	1101x	10111	00000	0000	00000	0000	0000
<i>Monapia silvatica</i>	10000	00011	00110	01110	00111	11120	21111	11000	0000	11000	0000	0000
<i>Monapia pichinahuel</i>	10000	00011	10110	01110	00101	11120	21111	11000	0000	11000	0000	0000
<i>Monapia huaria</i>	10000	00011	20111	01111	00110	110x0	32011	11000	0000	11000	0000	0000
<i>Monapia lutea</i>	10000	00011	20111	01111	00110	110x0	32011	11000	0000	11000	0000	0000
<i>Monapia charrua</i>	10101	00011	00000	01110	00101	10011	00111	00101	1111	00101	1111	1111
<i>Monapia guenoana</i>	11101	00011	00000	01010	1000?	11011	00111	00211	2111	00211	2111	2111
<i>Monapia angusta</i>	11101	0????	?0???	?????	?????	1?01-	00?11	00211	2111	00211	2111	2111
<i>Monapia fierro</i>	10000	00111	00000	01110	00001	1111-	00111	00000	1100	00000	1100	1100
<i>Monapia carolina</i>	10000	0????	?0???	?????	?????	11111	00111	00000	1100	00000	1100	1100
<i>Monapia tandil</i>	10000	00111	00000	01010	11000	?????	?????	??00?	0000	??00?	0000	0000

of 346 for $K = 3$, and a rescaled fit of 0.76. The same data were analyzed under equal weights, with the program NONA version 1.5.1 (Goloboff 1996b), and produced identical results.

The string of commands *poly-;max;apol;* of Pee-Wee/Nona was used to list the unambiguous synapomorphies common to the 270 possible dichotomous trees corresponding to the equally parsimonious resolutions of the politomies of the two trees. A parsimony jackknifing analysis (Farris et al. 1996) was made in order to have an estimation of support for clades. This procedure evaluates the stability of each node to a particular perturbation of the data set, which is the deletion of a portion of the characters. Over many replications with randomly deleted characters, the frequency at which a given node is monophyletic gives a measure of the support of the node: strongly supported nodes are more likely to be found even in absence of part of the data. The parsimony jackknifing is preferred over bootstrapping, because it produces a more direct relation between group frequency and support (Farris et al. 1996: 114). It is also preferred over the Bremer support (Bremer 1994), because in the latter, the values are absolute differences of steps (or fit), and a given figure might be originated by widely different relations among supporting and conflicting characters (Goloboff 1996a).

During the jackknifing analysis, 200 pseudoreplications were made deleting randomly 30% of the characters each time, as implemented in the JAK and FQ programs of Pee-Wee. Because the purpose was to evaluate support instead of quick searches, a more exhaustive search was made in each replication, instead of the kind of Wagner tree proposed in the original description of the method ("a fast approximate procedure, similar to the *hennig* command of Hennig86" (Farris et al. 1996: 113)). This procedure yields a better sensitivity of the support measure (Goloboff pers. comm.). For each pseudoreplicate matrix a Wagner tree with randomized sequence of addition of taxa was calculated and submitted to extended (TBR) branch-swapping, saving up to 50 most parsimonious trees (command *search=;*). Clades with positive support have a jackknife frequency between 0.5 and 1.

DISCUSSION

As in the previous analysis (Ramírez 1995b), *Monapia* appears supported by four characters (clade h, char. 18, 26, 28 and 32), of which two (char. 18 and 32) are also present in some taxa not included in this analysis. Compared with the previous fully resolved cladogram of *Monapia* species, this new analysis, with additional taxa and characters, is a bit more ambiguous. The consensus tree has a basal tetrachotomy; the resolutions place either clade j or *Monapia alupuran* as sister group of clade n.

Monapia tandil new species and *M. vittata* (clade i) are united by the prolateral denticles on the secondary conductor (char. 21), and the loss of the groove on the same sclerite (char. 17). *M. vittata* was previously considered the sister group of all other species of the genus, but in the present analysis its relationships are uncertain (see clade i), as those of *M. alupuran*, previously considered as the sister group of clade n. Clade j is united by the spinose forelegs and the median epigynal pouch (char. 29, 40 and 41), and clade k by the presence of a double anterior pouch (char. 27), with a convergence in clade p and in *M. alupuran*. Clade l is supported by four homoplasious characters: the flattened carapace and elongate abdomen (char. 2 and 4) are convergent in *Oxysoma*, the absence of apical ventral spines on fore tibiae and the strong ventral tibial spines (char. 42 and 43) are convergent in several groups, of which *Liparotoma* Simon 1884 and *Ferrieria* Tullgren 1901 are here included. The very similar species *M. guenoana* and *M. angusta* are united in the strongly supported clade m by five characters: the elongate carapace (char. 1), short third leg (char. 37), cheliceral spine (char. 38), and several ventral femoral spines on palp (char. 39) and first leg (char. 40 state 2). Clades n–q are unchanged from the previous analysis, although there are slight changes in the characters supporting them: the fusion of the secondary conductor to the tegulum (char. 22) is added as support to the clade n, the lobe on the unsclerotized area of secondary conductor is ambiguously optimized in clade p, one unclear state was deleted from character 14, and two logically dependent characters were considered here as one (see char. 31 above).

Clades l–q are strongly supported, with a

jackknife frequency of 0.9 or greater. The rather weak support of clade k, might be related only to the circumstance that *M. carolina* new species is known only from females.

Some of the species here described have a small sclerite arising from behind the median apophysis. Its shape can be pointed and thin (Figs. 27, 39), or triangular, or the sclerite can be apparently reduced to an indistinct sclerotized area. *Tasata* Simon 1903 species have a lamellar sclerite in that position, but its homology is unclear in most amaurobioidine genera. I preferred not to score or name this structure until a more detailed study across more amaurobioidine genera is done. In *M. fierro* and *M. tandil* the sclerite is pointed and thin. If this character is added to the matrix the same cladograms are obtained.

Areas of distribution of *Monapia* species might be of interest for studies of vicariance biogeography. *M. vittata*, *M. alupuran* and clade n are endemic to temperate forests of southern Chile and adjacent Argentina. Most species of clade n are sympatric. Only the sister species *M. lutea* and *M. huarua* appear to have non-overlapping distributions (Ramírez 1995b: 87): *M. lutea* ranges from Curicó Province to Chiloé, while *M. huarua* was found only in Valparaíso Province and around Santiago city. Clade l is endemic to riparian areas of eastern Argentina and Uruguay. *Monapia carolina* was found in central Argentina, where no other *Monapia* species lives. *M. fierro* and *M. tandil* are endemic to grasslands of east-central Argentina. Perhaps the most peculiar distribution is that of *M. vittata* and *M. tandil*, a pair of sister species known from widely disjunct areas. However, these data might change when additional specimens of *M. tandil*, known only from one individual, are collected. The cladogram presented here does not suggest a specific hypothesis of area relationship at both sides of the Andes because of the lack of resolution of the polytomy h: the six possible dichotomous resolutions propose mutually exclusive relationships of areas.

Monapia Simon 1897

Monapia Simon 1897: 93, 96, 97, 101. Gerschman de Pikelin & Schiapelli 1970: 131. Ramírez 1995b: 78.

Synonymy, diagnosis and description given in Ramírez 1995b.

Monapia charrua new species

(Figs. 7–13)

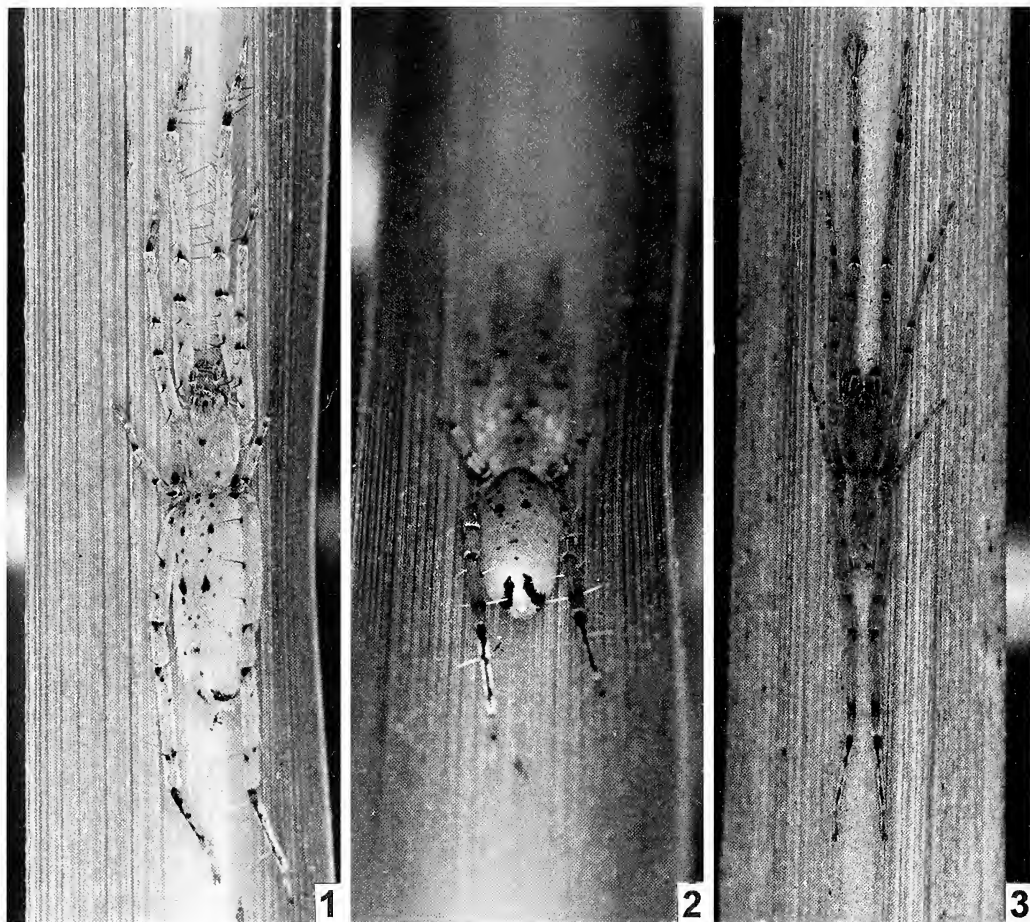
Types.—Female holotype (MACN 9576) and male paratype (MACN 9577) from Argentina, Entre Ríos Province, Río Gualaguaychú and RN 14, 14 July 1985, M. Ramírez.

Etymology.—The specific name is a noun in apposition taken from the Charrúas, an indigenous ethnic group that lived in the region where this species occurs.

Diagnosis.—Males, females and juveniles resemble those of *M. angusta* and *M. guenoana* by having an elongate body, but are distinguished by the chelicerae lacking spines.

Female (holotype).—Total length 6.63. Carapace 2.52 long, 1.68 wide, wider between coxae II–III. Length of tibiae/metatarsi: I missing; II 2.16/1.76; III 1.40/1.24; IV 2.72/2.72. Palpal tarsus 0.90 long. Sternum 1.50 long. Spines (female from Rosario del Tala): Leg I: Femur d 1-1-1, p 0-0-d1-1-d1 and an apical oblique line of thick setae (Fig. 7), r 0-d1-d1; tibia v 2-2-2-2-0, p and r 1-1; metatarsus v 2-2-2-0, p and r 1-0, d 0-p1-2. II: Femur d 1-1-1, p and r 0-1-1; tibia v 2-r1-2-0-2, p 1-1, r 1-v1; metatarsus v 2bas, p d1-1-0-1, r d1-v1-0-1, d p1-2. III: Femur d 1-1-1, p 0-1-1, r 1ap; tibia v p1-p1-2, p and r d1-1, d r1-1; metatarsus v 2-0-2, p and r d1-1-1, d p1-2. IV: Femur d 1-1-1, p and r 1ap; patella r 1; tibia v p1-2-2, p and r 1-1, d r1-1; metatarsus v 2-2-2, p, r and d = III. Palp: Femur ventrally with median line of 8 spines, d 0-0-1-p2, p 1ap; patella p 2-0, d 1-0-1; tibia p 2-2, d 1-1; tarsus v 2ap, p 1-1, r 1-0, d 2bas. Color: yellow with brown spots on the dorsal axis of body and sparse spots on dorsum (Fig. 8) and legs. Chelicerae with anterior longitudinal brown spot. Epigynum with anterior pouch wide, almost hemispherical, lateral lobes separate, median depression large, extended behind the anterior pouch (Fig. 12), usually occupied by a massive plug. Copulatory ducts with thick walls, accessory bulb with long duct parallel to margin of lateral lobes (Fig. 13).

Male (paratype).—Total length 4.12. Carapace 1.98 long, 1.28 wide. Abdomen 2.30 long. Length of tibiae/metatarsi: I 2.40/2.02; II 1.80/1.54; III 1.18/1.04; IV 2.06/2.22. Spines: Leg I: Femur d 1-1-1, p 0-0-d1-1-d1 and an apical oblique line of thick setae, r d1ap; tibia v 2-2-2-2-0, p and r 1-1; metatarsus v 2-2-2-0, p and r 1-0, d 0-p1-2. II: Femur



Figures 1–3.—*Monapia guenoana* new species. 1, Female on leaf of *Panicum prionitis*; 2, Same, posterior view; 3, Male.

d 1-1-1, p 0-d1-d1, r dlap; tibia v 2-r1-2-0, p and r d1-1; metatarsus v 2-r1-r1, p and r d1-1, d 0-p1-2. III: Femur = II; tibia v p1-p1-2, p and r d1-1, d r1-1; metatarsus v 2-0-2, p and r 0-d1-1, d 0-p1-2. IV: Femur d 1-1-1, p and r dlap; patella r 1; tibia v p1-2-2, p and r d1-1, d r1-1; metatarsus v 2-2-2, p and r d1-1-1, d 0-p1-2. Palp: Femur d 0-0-1-2, p dlap; patella p d2, d 1-0-1; tibia p 2-2, d r1-1; cymbium p 1-1-1, d 2-0. Color: as in female but darker. Copulatory bulb (Figs. 9–11) with paramedian apophysis sinuous, embolus long and thick, retrolateral portion of secondary conductor fused to tegulum.

Natural history.—Most specimens were collected on the large grass *Panicum prionitis* (“paja brava”) in temporarily flooded riparian areas, in close sympatry with *Monapia guenoana*.

Distribution.—Riparian zones of Entre Ríos Province in Argentina and Departamento Rocha in Uruguay.

Other material examined.—**ARGENTINA:** *Entre Ríos:* Same locality as types, 1♂1♀ (MACN); Gualeguay, 20 August 1989, M. Ramírez, 1♀ (MACN); Rosario del Tala, 20 November 1988, M. Ramírez, 1♀ (MACN). **URUGUAY:** *Departamento Rocha:* Arroyo Sarandí del Consejo, ruta 9 km 251, 18 May 1993, M. Ramírez & F. Pérez Miles, 1♂3juv. (MACN).

Monapia guenoana new species
(Figs. 1–3, 14–19)

Types.—Female holotype (MACN 9578) and male paratype (MACN 9579) from Argentina, Entre Ríos Province, Gualeguay, 20 August 1989, M. Ramírez.

Etymology.—The specific name is a noun

in a position taken from the Guenoanes, an indigenous ethnic group related to the Charrúas, that lived in the region where this species occurs.

Diagnosis.—Males, females and juveniles resemble those of *M. angusta* and *M. charrua* by having an elongate body, but are distinguished by the anterior legs with several ventral spines on femora (Fig. 14), and numerous (more than 7 pairs) strong ventral spines on tibiae.

Female (holotype).—Total length 6.95. Carapace 2.38 long, 1.46 wide, wider on coxa II. Length of tibiae/metatarsi: I 2.96/1.54; II 1.60/1.04; III 0.90/0.68; IV 2.76/2.08. Palpal tarsus 0.80 long. Sternum 1.38 long. Spines: Chelicerae with 1 strong basal anterior. Leg I (Fig. 14): Femur d 1-1-1, p 1 ap, v 2-2-2-2ap or 2-2-2-2-r1-r1-r1ap; tibia ventrally with a prolateral line of 10 or 11, and a retrolateral of 13 or 14; metatarsus v 2-2-2-0, p y r 1 ap. II: Femur d 1-1-1, p and r 1 ap; tibia v r1-r1-r1-2-0; metatarsus v 2-r1-r1, p 0-1-d1, r d1ap. III: Femur = II; tibia v p1-p1-0, p 1-1, r 0-1, d r1-0-1; metatarsus v r1-0, d 2ap, r 1ap. IV: Femur d 1-1-1, p 0-1; tibia v p1-2-r1, p and r 1-1, d r1-0-1; metatarsus v 2-p1-0, p 2-0-1, r 1-1-2. Palp: Femur ventrally with median line of 4 or 7, d 0-0-1-1, p 1ap; patella d 1ap, p 2bas; tibia p 3-2, d 1-1; tarsus d 2bas, p 1, v 2ap. Color: yellow, with dorsal pattern of brown spots (Figs. 1, 2) and two dark parallel patches at each side of spinnerets. Legs with spots as follows: femora I-IV d 1-1-1-1, III p v1ap; patellae I-IV d 3-1, III v p1 wide; tibiae I-III d 1bas, IV d 1-1, p 0-1, r 1-0; metatarsi I-III d 1-1, IV with a longitudinal band, basally wider. The terminal dark spots on abdomen and the lines on hind metatarsus are conspicuous from above when the spider is at resting position (Fig. 2). Epigynum with anterior pouch wide, lateral lobes separate, median area depressed behind the anterior pouch (Fig. 18), copulatory openings usually occupied by one plug each. Copulatory ducts with thick walls, duct of the accessory bulb curved in a transversal plane (Fig. 19).

Male (paratype).—Total length 3.20. Carapace 1.80 long, 1.16 wide. Abdomen 2.08 long. Length of tibiae/metatarsi: I 2.84/1.78; II 1.54/1.02; III 0.80/0.64; IV 2.48/1.88. Spine arrangement similar to female, but much weaker. Ventral foreleg spines thin and not erect. Color: as in female; some individuals

have dark first tibiae. Copulatory bulb (Figs. 15–17) with paramedian apophysis sinuous, embolus short and thick, with basal membrane extending half of its length, retrolateral portion of secondary conductor small, with a ventro-basal peak, prolateral portion without groove, displaced towards the base of embolus.

Natural history.—Specimens were collected at the bases of the large grass (1.5–2 m tall) *Panicum prionitis* (“paja brava”) in temporarily or permanently flooded riparian areas. In some localities they occur in close sympatry with *Monapia charrua*. Females make a flattened egg-sac on the concave side of the leaves, and the egg-sac is covered by its cryptic body. The grasses where the spiders live have thin, quite rigid and straight leaves, with a V-section. The spider uses to walk along the concavity of the leaf keeping its legs I, II and IV aligned with the body and leaf axis (Figs. 1–3). While doing this, the forelegs are usually not used to walk, but to palpate the substrate, and the articulations femur-patella of legs II and IV are almost not moved. In these legs the movements are mostly achieved by the tibia-metatarsus joints.

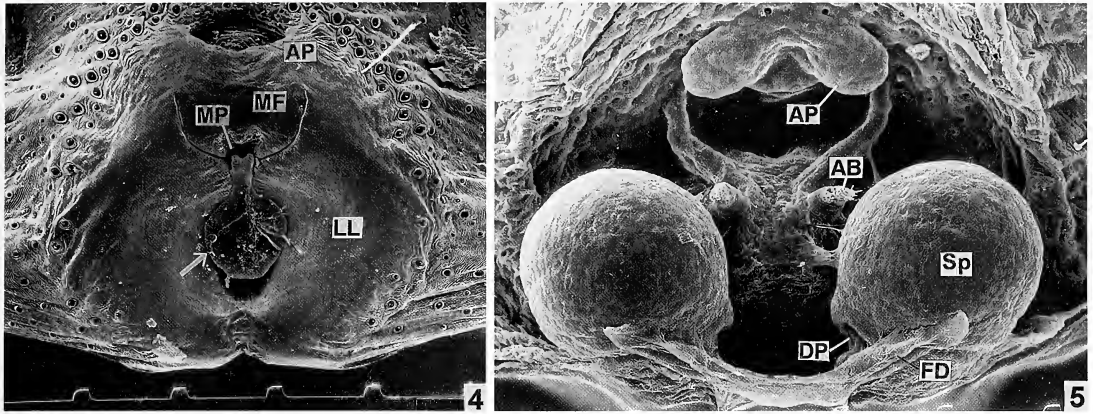
Distribution.—Riparian zones of Entre Ríos and northeast of Buenos Aires Provinces in Argentina, and Departamento Rocha in Uruguay.

Other material examined.—**ARGENTINA:** *Entre Ríos:* Same data as the types, 2♀ (MACN); Arroyo El Palmar and RN 14, 14 October 1984, M. Ramírez, 1♀ (MACN); Arroyo Gualeacán and RN 14, near Gualeguaychú, 2 November 1996, M. Ramírez 2♂2♀ (MACN); Río Gualegachú and RN 14, 10 December 1982, M. Ramírez & P. Goloboff, 3♀ (MACN); Rosario del Tala, 20 November 1988, M. Ramírez, 3♀ (MACN). *Buenos Aires:* Delta, estación experimental INTA, July 1968, A. Bachmann, 1♀ (MACN); Isla Talavera, 2 km E Zárate, 3 November 1996, M. Ramírez 1♂4♀ (MACN). **URUGUAY:** *Departamento Rocha:* Arroyo Sarandí del Consejo, ruta 9 km 251, 18 May 1993, M. Ramírez & F. Pérez Miles, 1♀3juv. (MACN).

Monapia angusta (Mello-Leitão 1944) **new combination**
(Figs. 20–23)

Arachosia angusta Mello-Leitão 1944: 357 (juvenile holotype from Argentina, Buenos Aires Province, Tigre, Río Guayracá, MLP 16100, examined).

Note: The holotype is a badly preserved and slight-



Figures 4–5.—*Monapia fierro* new species. 4, Epigynum (arrow indicates the copulatory plug on median depression); 5, Vulva, dorsal. (AB = Accessory bulb. AP = epigynal anterior pouch. DP = “dictynoid” pore of spermatheca. FD = fertilization duct. LL = epigynal lateral lobe. MF = epigynal median field. MP = epigynal median pouch. Sp = spermatheca.)

ly crushed juvenile. Although the cheliceral spines are lost, their insertions are clearly visible, as well as the ventral spines on the foreleg.

Diagnosis.—Females and juveniles resemble those of *M. guenoana* by having an elongate body and basal anterior spines on the chelicerae, but can be distinguished by having only 4 pairs of ventral spines on the anterior tibiae.

Female (Mar del Tuyú).—Carapace damaged, bowed, ≈ 2.50 long, ≈ 1.70 wide. Abdomen elongated, deformed. Length of tibiae/metatarsi: I 3.40/2.48; II 2.26/1.64; III 1.28/1.20; IV 3.32/2.56. Palps long (Fig. 20), palpal tarsus 1.30 long. Sternum 1.44 long. Spines: Chelicerae with 1 strong basal anterior. Legs I: Femur d 1-1-1, p 0-0-v1-d1 and an apical oblique line of thick setae, r 1ap; tibia v 2-2-2-2-0, d r1-1 setae; metatarsus v 2-2-2-0-0, d p1-p1-r1-0-2. II: Femur d 1-1-1, p 0-1-1, r 1ap; tibia v 2-r1-2-r1-0, p 1-1, d r1-1 setae; metatarsus v 2-r1-r1, p 1-0, d p1-2. III: Femur = II; tibia v p1-p1, p 0-1, d r1-1; metatarsus v 2-0-p1, d p1-2. IV: Femur d = I; tibia v 2-p1-r1, p and r 1-1, d r1-1; metatarsus v 2-p1-p1, p 1-1, r 0-1, d 2-2-2 or 2-p1-2-2. Palp: Femur with ventral and prolateral lines of several spines, d 0-0-1-1-1, p 0-1; patella p 2-3, d 1-1; tibia with a ventral line of slender spines, p 3-1-d1-0-0, d 1-1-0; tarsus v 2-2-2, d p2bas. Color (immature from Castillos, Fig. 21): yellow, with dark reddish-brown spots on legs and dorsum; abdomen with dorsal white guanine reticulum under cuticle. Epigynum

with lateral lobes widely separated, median field depressed in the center and behind the lateral lobes, folded in its anterior half and elevated over the anterior pouch (Fig. 22). Anterior pouch with spherical cavity; the opening is prolonged on each side in the anterior border of the median field. Spermathecae oval, accessory bulbs with long and sinuous ducts (Fig. 23).

Male.—Unknown.

Natural history.—The specimens were collected on Pampas grass *Cortaderia seloana* (“cortadera”).

Distribution.—Margins of Río de La Plata and Paraná in Buenos Aires and Uruguay.

Other material examined.—**ARGENTINA:** *Buenos Aires:* Mar del Tuyú, February 1984, M. Ramírez 1♀ (MACN); *Paraná de las Palmas,* 7 April 63, M. Galiano, 2juv. (MACN); *Reserva Otamendi,* 10 June 1997, M. Ramírez, L. Compagnucci, C. Grismado, F. Uehara, 1juv. (MACN). **URUGUAY:** *Departamento Rocha:* Laguna de Castillos, 19 May 1993, M. Ramírez & F. Pérez Miles, 4juv. (MACN).

Monapia fierro new species
(Figs. 4, 5, 24–30)

Types.—Female holotype (MACN 9580) and male paratype (MACN 9581) from Argentina, Buenos Aires Province, Sierra de la Ventana, Cerro Negro, April 1974, Cesari.

Etymology.—The specific name is dedicated to the brave gaucho Martín Fierro, who

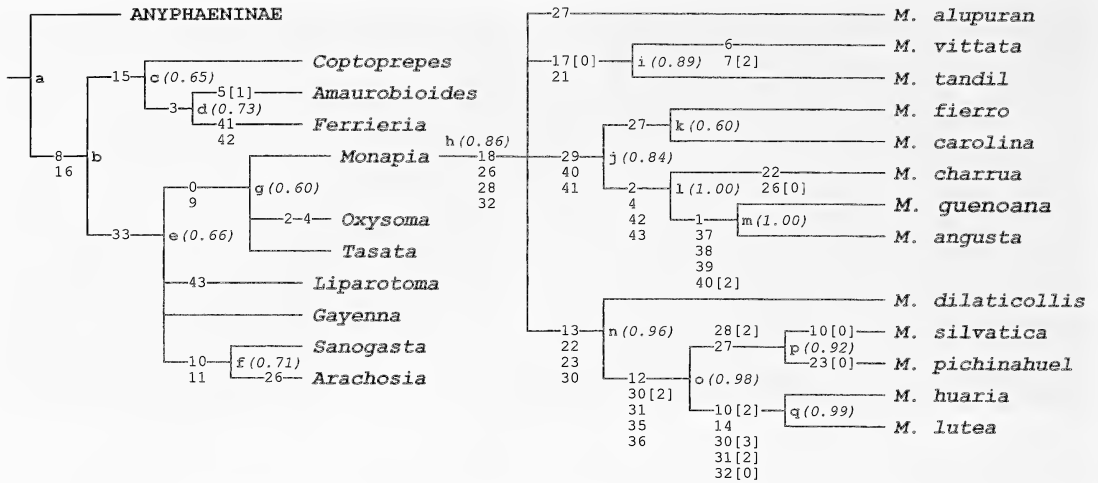


Figure 6.—Cladogram of *Monapia* species and outgroups. Unambiguous synapomorphies are noted on branches, character states are "1", otherwise noted in brackets. Jackknife frequency for each clade noted in parenthesis.

gives the name to the most popular Argentinian poem, written by José Hernández.

Diagnosis.—This species is most similar to *M. carolina*, but females can be distinguished by the wider opening of the anterior epigynal pouch; furthermore, they usually have 5 pairs of ventral spines on anterior tibiae. Males are recognized by the short and thick embolus.

Female (holotype).—Total length 6.00. Carapace 2.88 long, 2.10 wide, wider on coxae III. Length of tibiae/metatarsi: I 2.06/1.72; II 1.80/1.60; III 1.54/1.58; IV 2.20/2.56. Palpal tarsus 1.00 long. Sternum 1.50 long. Spines: Legs I: Femur d 1-1-1, p 0-0-1-d1, r 1ap; tibia with two lines of ventral spines, 4 or 6 prolateral, 5 retrolateral, (most commonly 2-2-2-2-0-2), p 1-1, r 0-1; metatarsus v 2bas, p and r 1, d 0-p1-2. II: Femur d 1-1-1, p and r 0-1-1; tibia v 2-2-2-0-2 or 2-2-2-2-2, p 1-1, r 0-1; metatarsus = I. III: Femur = II; patella r 1, d 1ap; tibia v p1-2-2, p and r 1-1, d r1-1; metatarsus v 2-0-2, p and r 1-1, d 2-p1-2. IV: Femur d 1-1-1, p and r 1ap; patella r 1, d 1ap; tibia = III; metatarsus v 2-2-2, p and r 1-1, d 2-p1-2. Palp: Femur d 0-0-1-2, p 1ap; patella d 1-1; tibia p 2-2, d 1-1; tarsus v p2ap, p 1-1, r 1-0, d 2bas. Color: light brown, legs with brown spots, dorsum with brown pattern as in Fig. 25, sternum with three spots on each side, abdomen ventrally with three longitudinal brown stripes from epigastric furrow to the spiracle. Epigynum with central depression, lateral lobes with internal border sinuous, al-

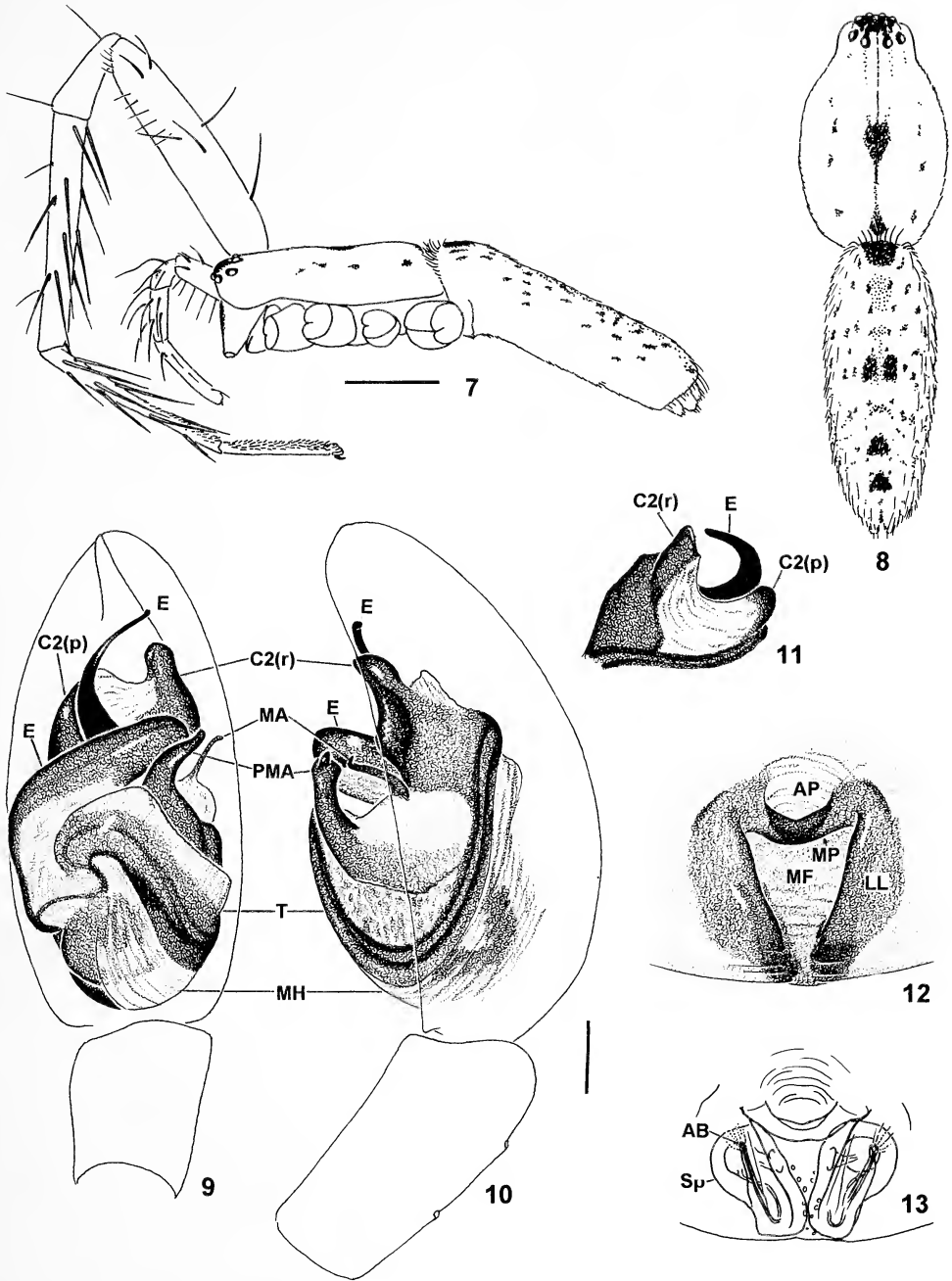
most touching on middle (Figs. 4, 29); median field elevated below anterior pouch, central depression prolonged in small foldings above central depression. Anterior pouch with two-fold cavity (Figs. 5, 30). Accessory bulbs with vertical ducts. Central epigynal depression often occupied by hard plug (Fig. 4).

Male (paratype).—Total length 5.41. Carapace 2.52 long, 1.90 wide. Abdomen 2.80 long. Length of tibiae/metatarsi: I 1.98/1.70; II 1.68/1.48; III 1.40/1.40; IV 1.98/2.20. Spines distributed as in female but weaker. Color: as in female. Cymbium with slight retrolateral basal notch. Copulatory bulb (Figs. 26–28) with paramedian apophysis short and thick, embolus short and thick, with basal membrane extending half of its length, retrolateral portion of secondary conductor with long and thin tip and small ventro-basal peak. There is a thin pointed sclerite of uncertain homology arising behind the median apophysis.

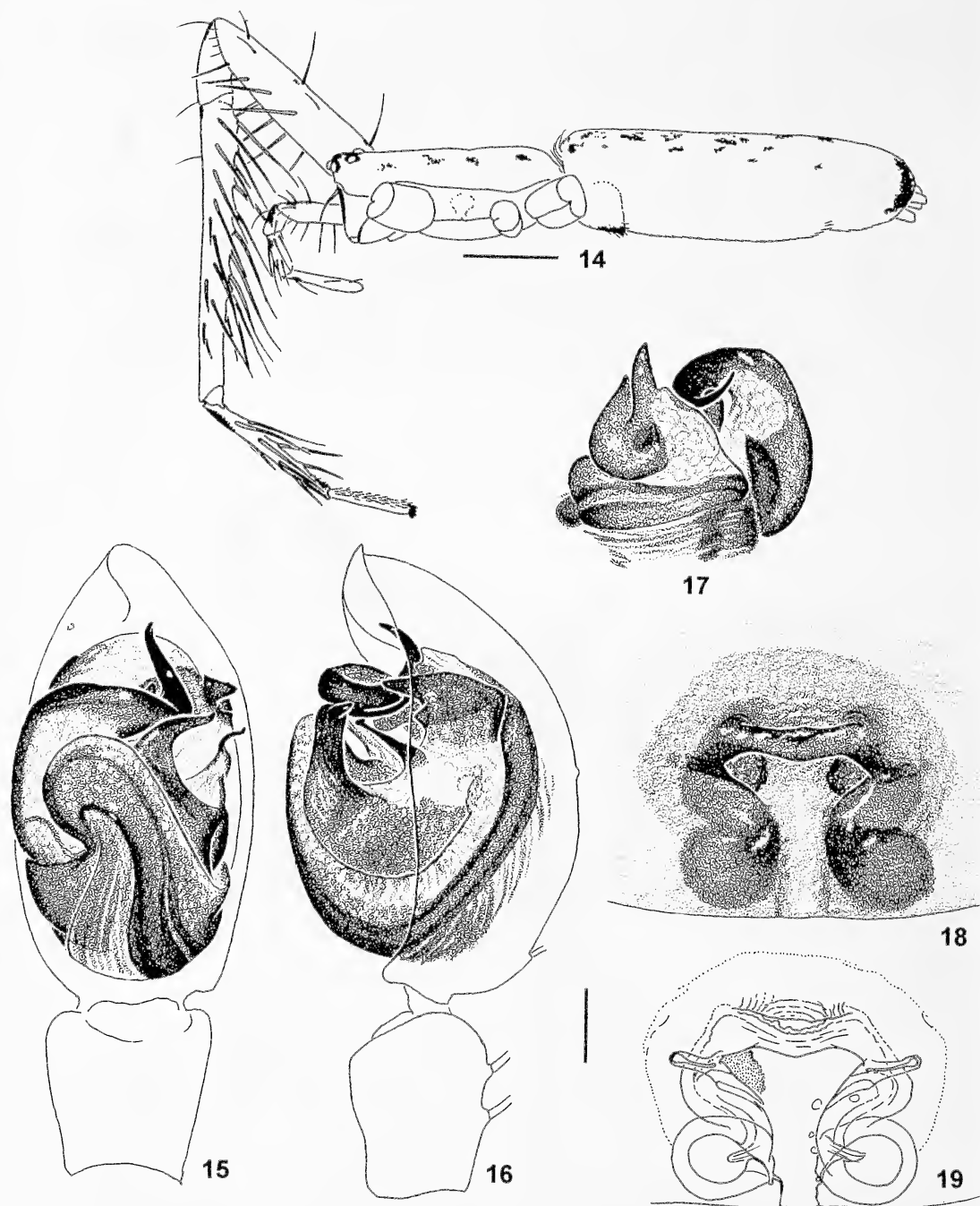
Natural history.—Specimens were collected in white retreats in bunches of grass.

Distribution.—Known from grasslands in Buenos Aires and eastern Chubut Provinces.

Other material examined.—**ARGENTINA:** *Chubut*: Isla de los Pájaros, Golfo de San José, 10 August 1975, M. Rumboll, 3♀ (MACN); *Península de Valdez*, Punta Norte, 2 August 1972, M. Rumboll, 1♀ (MACN). *Buenos Aires*: same locality as types, 2♂2♀ 1juv. (MACN); Allen, August 1945, Conciotti, 1♀ (MLP); Argerich, Villarino, June-July



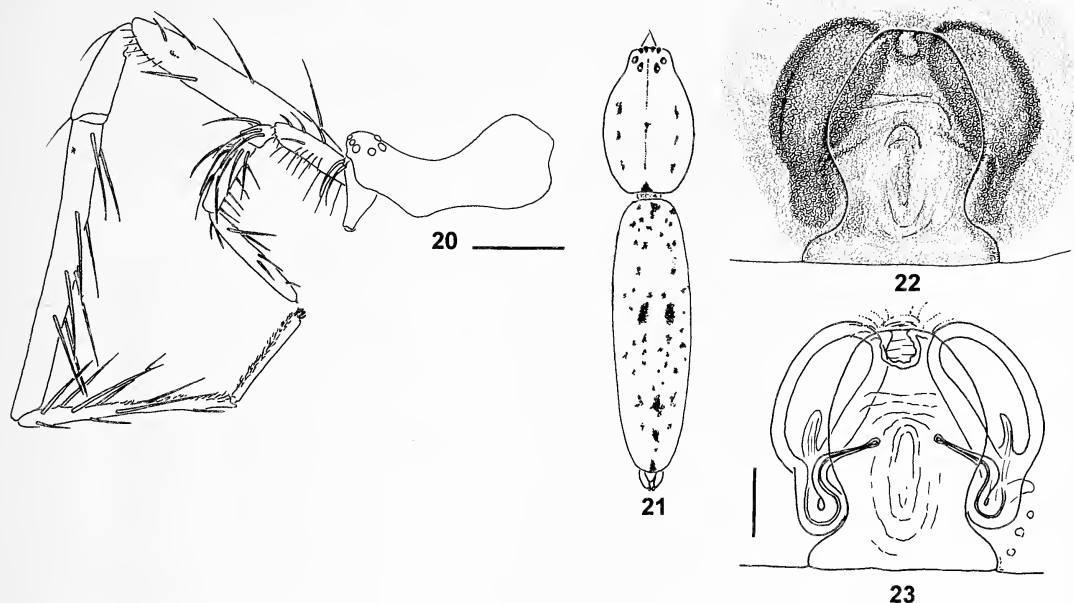
Figures 7–13.—*Monapia charrua* new species. 7, Female, lateral; 8, Female, dorsal; 9, Male palp, ventral; 10, Palp, retrolateral; 11, Palp, apical detail; 12, Epigynum, ventral; 13, Epigynum, dorsal, cleared. Abbreviations: AB = Accessory bulb of spermathecae; AP = epigynal anterior pouch; C2(p) = prolateral portion of the amaurobioidine secondary conductor; C2(r) = retrolateral portion of the amaurobioidine secondary conductor; E = embolus; LL = epigynal lateral lobe; MA = median apophysis; MH = median hematocha; MF = epigynal median field; MP = epigynal median pouch; PMA = amaurobioidine paramedian apophysis; Sp = spermatheca; T = tegulum. Scales: Figs. 7–8 = 1 mm, Figs. 9–13 = 0.1 mm.



Figures 14–19.—*Monapia guenoana* new species. 14, Female, lateral; 15, Male palp, ventral; 16, Palp, retrolateral; 17, Palp, apical detail; 18, Epigynum, ventral; 19, Epigynum, cleared. Scales: Fig. 14 = 1 mm, Figs. 15–19 = 0.1 mm.

1958, H. Hepper, 2♀ (MACN); Brandsen, no date, M. Birabén, 1♀ (MLP); D'Orbigny, November 1963, J.M. Gallardo, 1♀ (MACN); 15 Km W Lobería, 4 September 1972, 1♀ (MACN); Las Flores, 24 May 1931, J.M. Daguerre, 5♂14♀ (MACN

29951); Los Médanos, 8 April 1965, J.M. Gallardo & E. Maury, 2♂ 5juv. (MACN); Mar del Plata, 20–21 July 1984, M. Ramírez, 8♀ (MACN); Mar del Tuyú, 2 May 1981, M. Ramírez, 1♂ (MACN); Olavarría, Sierra de la China, 19 November 1965, E.



Figures 20–23.—*Monapia angusta* (Mello-Leitão). 20, Female, lateral; 21, Immature from Castillos; 22, Epigynum, ventral, 23, Epigynum, cleared. Scales: Figs. 20–21 = 1 mm, Figs. 22–23 = 0.1 mm.

Maury, 3 ♀ 1 juv. (MACN); Otamendi, 20 October 1979, P. Goloboff, 1 ♀ (MACN); Quequén, 7–12 May 1931, J.M. Daguerre, 1 ♂ 6 ♀ (MACN 28871), June 1931, J.M. Daguerre, 1 ♂ 1 ♀ (MACN), 1941, E. Balech, 1 ♂ (MACN); Río Luján, estación FCGM, 14 November 1991, Pesce, 1 ♀ (MACN); Rosas (?), F.C.S., 2 ♀ (MACN); between Tres Arroyos and Pringles, November 1962, M.E. Galiano, 4 ♀ (MACN); Sierras de Azul, 1–2 October 1983, P. Goloboff & A. Zanetic, 1 ♀ (MACN); Sierra de la Ventana, Pque. Prov. E. Tornquist, 18–20 November 1982, M. Ramírez, 5 ♀ (MACN); October 1988, M.E. Galiano & C. Scioscia, 1 ♀ (MACN); Sierra de los Padres, 27 October 1984, M. Ramírez, 10 ♀ (MACN); Tandil, J.M. Viana, many ♂ ♀ (MACN); Tornquist, estación Fortín Chaco, January 1972, J. Arias, 1 ♀ (MACN).

***Monapia carolina* new species**
(Figs. 31–34)

Types.—Female holotype (MACN 9582) from Argentina, San Luis Province, Carolina, September 1970, J.M. Viana & Williner.

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—This species is most similar to *M. fierro*, but females can be distinguished by the small opening of the anterior epigynal

pouch; furthermore, the anterior tibiae usually bear 6 pairs of ventral spines (Fig. 32).

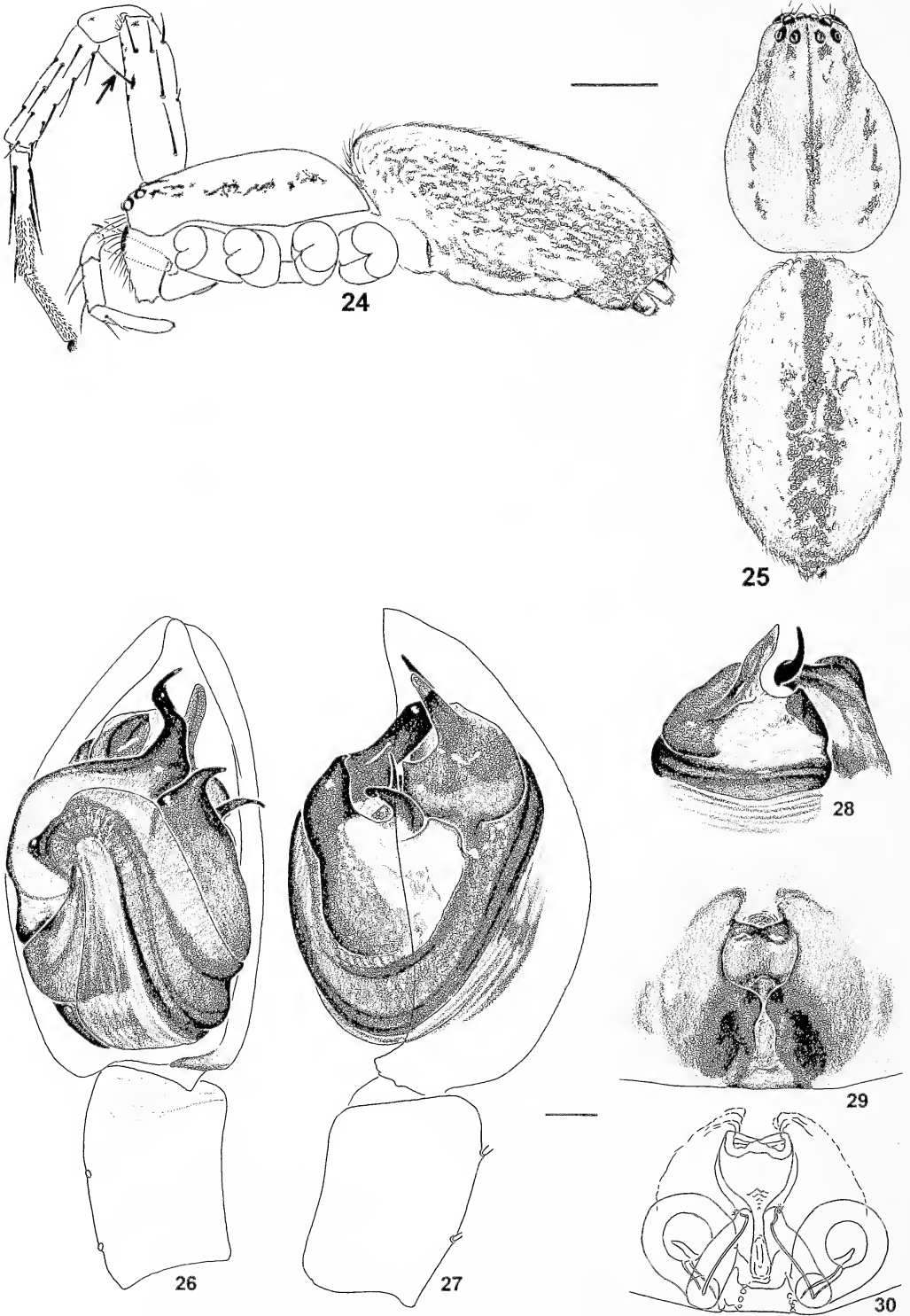
Female (holotype).—Total length 6.38. Carapace 2.80 long, 2.00 wide, wider on coxae III. Abdomen 3.88 long. Length of tibiae/metatarsi: I 1.92/1.58; II 1.70/1.44; III 1.44/1.48; IV 2.10/2.40. Palpal tarsus 0.94 long. Sternum 1.50 long. Spines as in *M. fierro*, but usually 2-2-2-2-2-0-2 ventral spines on tibia I. Color: light brown with brown spots and patches (Fig. 31), legs with brown spots at spine bases, and ventral spot lines on femora: one retrolateral on I and II, two on III, and one prolateral on IV; abdomen ventrally light, with short median band of brown spots. Epigynum with separate lateral lobes, median area elevated above anterior pouch, central depression deep, extended forward in central pouch (Fig. 33). Anterior pouch twofold, with conical cavities directed to each side (Fig. 34), accessory bulbs with ducts vertical to oblique.

Male.—Unknown.

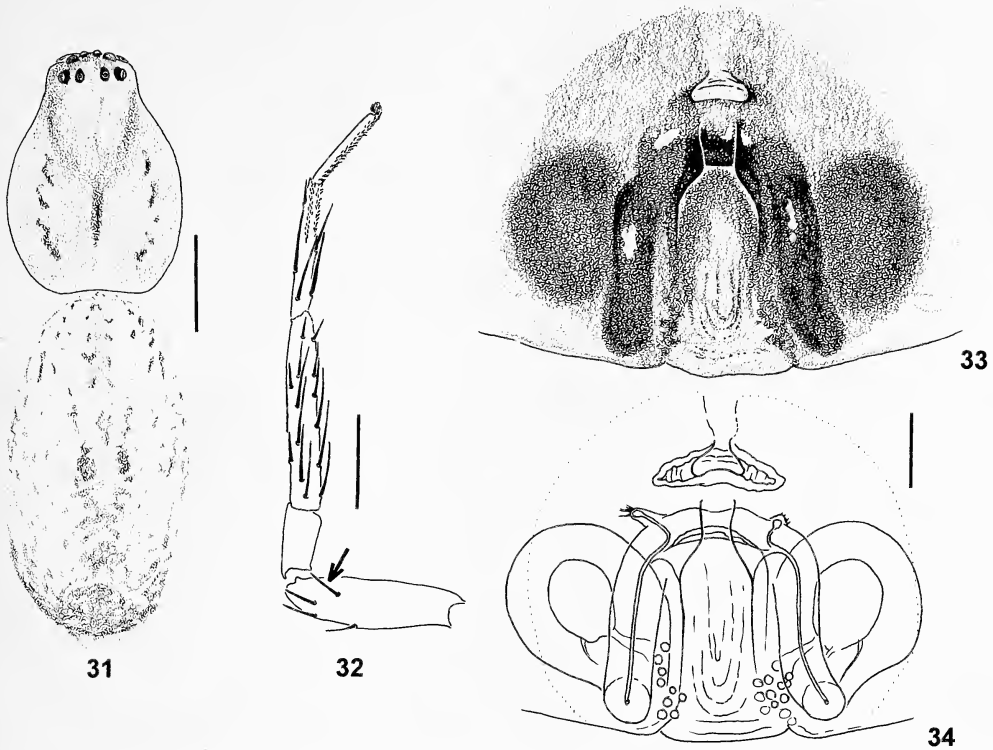
Natural history.—Unknown.

Distribution.—Known from Córdoba and San Luis Provinces.

Other material examined.—ARGENTINA:



Figures 24–30.—*Monapia fierro* new species. 24, Female, lateral (arrow indicates prolateral/ventral spine on femur); 25, Female, dorsal; 26, Male palp, ventral; 27, Palp, retrolateral; 28, Palp, apical detail; 29, Epigynum, ventral; 30, Epigynum, cleared. Scales: Figs. 24–25 = 1 mm, Figs. 26–28 = 0.1 mm.



Figures 31–34.—*Monapia carolina* new species. 31, Female, dorsal; 32, Left foreleg (arrow indicates prolateral/ventral spine on femur); 33, Epigynum, ventral; 34, Epigynum, cleared. Scales: Figs. 31, 32 = 1 mm, Figs. 33, 34 = 0.1 mm.

Córdoba: La Cumbre, 8 November 1991, M. Ramírez, 1 ♀ (MACN); Pampa de Achala, El Cóndor, 20 November 1983, M.E. Galiano, 1 ♀ (MACN). *San Luis*: same locality as types, 3 ♀.

Monapia tandil new species
(Figs. 35–39)

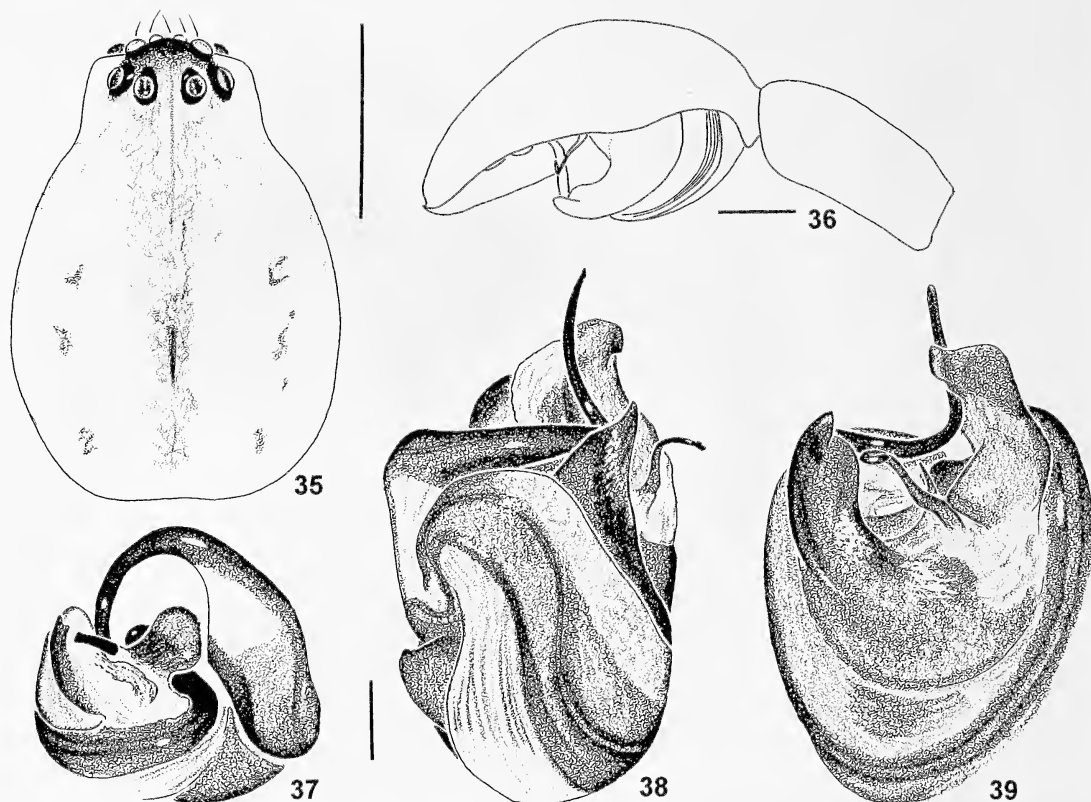
Types.—Male holotype (MACN 9583) from Argentina, Buenos Aires Province, Tandil, no date, J.M. Viana.

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—This species is closest to *M. vittata*, as both have a flat apical extension on the amaurobioidine paramedian apophysis, and can be easily distinguished from *M. vittata* by the thin median apophysis.

Male (holotype).—Total length about 5.60. Carapace 2.50 long, 1.80 wide, wider on coxae III. Abdomen badly preserved, about 3.10 long. Length of tibiae/metatarsi: I 3.46/3.03; II 2.73/2.30; III 1.97/1.70; IV 2.87/2.97. Spines: I: Femur d 1-1-1, p and r 0-1-1; tibia

v 2-2-2, p and r 1-1; metatarsus v 2bas, p and r 1, d 0-p1-2. II=I. III: Femur d 1-1-1, p 0-0-1-1-1, r 0-1-1; tibia v p1-2-2, p and r 1-1, d 0-1; metatarsus v2-p1-2, p and r d1-1-1, d 0-p1-2. IV: Femur d 1-1-1, p 1ap, r 0-1-1; patella r 1; tibia and metatarsus = III. Palp: Femur d 0-0-1-p3; patella d 1ap; tibia p 2-2, d 1-1; cymbium p 0-1-1. Color: light brown with brown pattern on carapace as in Fig. 35, legs with brown spots, tibiae III and IV darker, with two longitudinal light lines; sternum with one oval brown patch in front to each coxae I–III, and median longitudinal line; abdomen light gray, with brownish-violet anterior median patch, several inverted “V” through the median line, the three posterior darker, and a very dark patch upon the anal tubercle. Cymbium with slight retrolateral basal notch (Fig. 36). Copulatory bulb (Figs. 37–39) with paramedian apophysis short and thick, prolateral portion of secondary conductor without groove, displaced towards the base of embolus and bearing small denticles. There is a thin,



Figures 35–39.—*Monapia tandil* new species. 35, Male carapace; 36, Male palp, retrolateral; 37, Male palpal bulb, apical detail; 38, Palp, ventral; 39, Palp, retrolateral. Scales: Fig. 35 = 1 mm, Fig. 36 = 0.2 mm, Figs. 37–39 = 0.1 mm.

curved and pointed sclerite of uncertain homology arising behind the median apophysis.

Natural history.—Unknown.

Distribution.—Known only from type locality.

Other material examined.—None.

Monapia dilaticollis (Nicolet 1849)

Clubiona dilaticollis Nicolet 1849: 436.

M. dilaticollis, Ramírez 1995b: 78.

Additional records.—**CHILE:** *REGION IX:* Malleco: Río Blanco, Curacautín, 1–5 February 1959, L. Peña, 1 ♀ (IRSN I.G. 19736). *Unknown locality:* El Coigo, 1–10 October 1960, L. Peña, 1 ♀ (IG 19736, IRSN).

Monapia vittata (Simon 1884)

Tomopisthes vittatus Simon 1884: 135.

Monapia vittata, Ramírez 1995b: 81.

Additional records.—**ARGENTINA:** *Chubut:*

La Hoya, 42°54'S, 71°19'W, 16 November 88. V. & B. Roth, 5 ♀ (CAS).

Monapia lutea (Nicolet 1849)

Clubiona lutea Nicolet 1849: 429.

Monapia lutea, Ramírez 1995b: 86.

Additional records.—**ARGENTINA:** *Neuquén:* P. Nac. Lanín: 5 km E Hua Hum, 5 November 1981, Pucará, Nielsen & Karsholt, 5 ♂ 8 ♀ (ZMK); February 1963, S. Schajovskoy, 1 ♀ (MACN); November 1971, L. Yinoff, 1 ♀ (MACN); December 1973, S. Schajovskoy, 2 ♂ (MACN); San Martín de los Andes, 640 m, 17–31 October 1981, Nielsen & Karsholt, 2 ♂ (ZMK). *Río Negro:* Bariloche, 12–20 November 1981, Nielsen & Karsholt, 1 ♀ (ZMK); 810 m, 22 November 1978, Nielsen & Karsholt, 1 ♀ (ZMK); El Bolsón, 24 November 1962, Birabén, 6 ♂ 6 ♀ (MACN); February 1965, Birabén, 1 ♀ (MACN); *Chubut:* P. Nac. Lago Puelo, 220 m, 18 November 1978, Misión Científica Danesa, 1 ♂ (ZMK); Parque Nacional Los Alerces: March 1974, Bordon, 1 ♀ (MACN); Lago Futalaufquen, January 1990, M.J. Ramírez, 5 ♀ (MACN); Lago Menéndez,

Río Arrayanes, February 1986, M. Ramírez, 6♀ (MACN); Villa Futalaufquen, 9 February 1986, M. Ramírez, 1♀ (MACN). **CHILE: REGION VIII:** Concepción: Hualpén, 2 January 1989, M. Ramírez, 1♀ (MACN). **REGION IX:** Malleco: Fundo María Ester, 15 km W Victoria, 14 January 1989, M. Ramírez, 2♀ (MACN); Monumento Natural Contulmo, 12 January 1989, M. Ramírez, 1♀ (MACN). Unknown locality: El Coigo, 1–10 October 1960, L. Peña, 1♀ (IG 19736, IRSN); 36, 1♀ (IG 15.765, IRSN). **REGION X:** Valdivia: 18.20 km NW Neltume, 25 November 1988, V. & B. Roth, 1♀ (CAS). Osorno: P. Nac. Puyehue, Aguas Calientes, 40°44'S, 72°19'W, 1440 m, 5–7 December 1988, V. & B. Roth, 2♀ (CAS).

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THE FEMALES OF *ANELOSIMUS DUBIOSUS* AND *ANELOSIMUS JABAQUARA* (ARANEAE, THERIDIIDAE)

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ABSTRACT. The females of *Anelosimus dubiosus* Keyserling 1891 and *Anelosimus jabaquara* Levi 1956 are described and illustrated based on specimens collected in Jundiá, São Paulo, Brazil.

Keyserling (1891) described *Anelosimus dubiosus* based on a male collected in Nova Friburgo, Rio de Janeiro, Brazil. Levi (1956) described *Anelosimus jabaquara* also based on a male. This latter species, however, was considered a junior synonym of *A. dubiosus* by the same author in 1963 (Levi 1963). Levi & Smith (1982) revalidated *A. jabaquara*, but until now the two species were known only from males.

Both species build communal webs of similar size and architecture and are sympatric in some places, as in Serra do Japi, a forest reserve close to Jundiá, São Paulo, Brazil. During studies on the ecology of social spiders in this area, we encountered these and three other species of the genus, *A. jucundus* (O.P.-Cambridge 1896), *A. ethicus* (Keyserling 1884) and *A. studiosus* (Hentz 1850).

Adult males of *A. jabaquara* and *A. dubiosus* are found in colonies only during the reproductive period. During the rest of the year the identification of the species is based on the females, which are described in this paper.

METHODS

The format of the description follows Levi (1963). Complete measurements were taken from one specimen of each species, and additional measurements of total length, carapace length and width were taken from six specimens of each species. All measurements are in mm. The epigyna were observed and drawn using an Olympus SZH10 dissecting microscope. For observation of the internal genitalia, the epigyna were immersed and examined in clove oil and drawings were made using an Olympus Bx50 microscope with a camera lucida attached. Coloration was de-

scribed using specimens that had been fixed for two days. The material is deposited in the collection of Instituto Butantan, São Paulo (IBSP, Curator: A.D. Brescovit).

Anelosimus dubiosus (Keyserling 1891)
(Figs. 1-3)

Theridium dubiosum Keyserling 1891: 187, pl. 6, fig. 133 (Male holotype from Nova Friburgo, Rio de Janeiro, Brazil, in British Museum of Natural History, not examined)

Anelosimus dubiosus: Levi 1963: 34; Levi & Smith 1982: 277, fig. 4

Diagnosis.—*Anelosimus dubiosus* males can be distinguished from all other species of *Anelosimus*, except *A. jabaquara*, by the presence of a half-moon shaped tegular process. This species differs from *A. jabaquara* by the long and filamentous embolus (Levi & Smith 1982, fig. 4). The females are similar to *A. jucundus* and *A. jabaquara* in coloration and shape of the epigynum, but can be separated from these and other species of the genus by the lateral loops of copulatory ducts (Fig. 3).

Description.—*Female*: Carapace red with black rings around the eyes, clypeus and chelicerae orange, sternum and labium red, endites orange. Legs light brown with distal ends of segments darker, tibiae and femora with dark rings in the middle. Abdomen light brown with a dorsal median band with black spots (Fig. 1) ending with four transverse red strips, venter with a central dark band with a black ring around spinnerets. Posterior median eyes little more than their diameter apart, slightly less from laterals. Epigynum a lightly sclerotized, folded plate, with a small posterior projection (Fig. 2). Total length 4.29, carapace 1.65 long and 1.12 wide. First femur

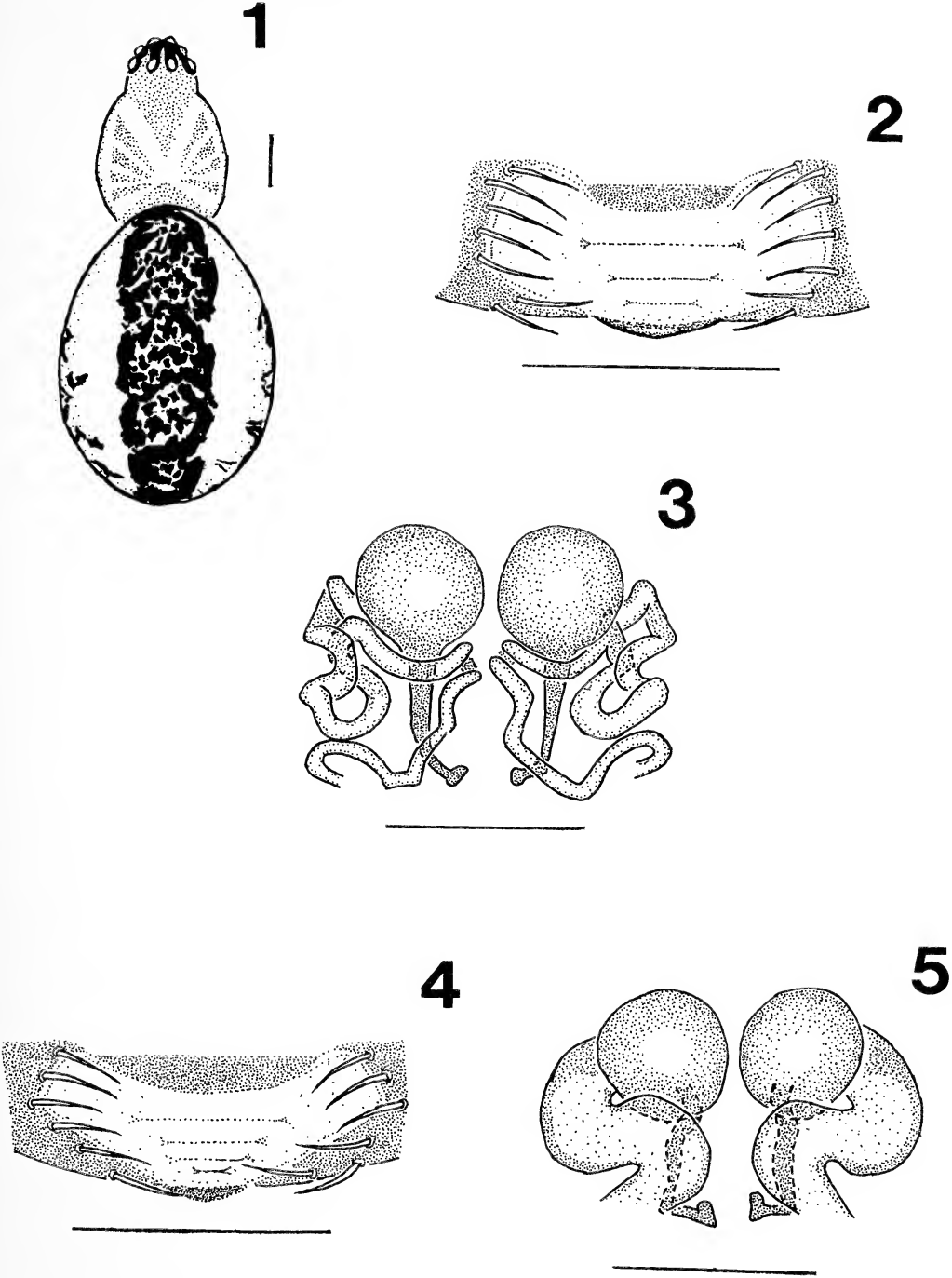


Figure 1–5.—*Anelosimus dubiosus* and *Anelosimus jabaquara*. 1. *A. dubiosus*, dorsal view of carapace and abdomen; 2. *A. dubiosus*, epigynum, ventral view; 3. *A. dubiosus*, internal genitalia, dorsal view; 4. *Anelosimus jabaquara*, epigynum, ventral view; 5. *A. jabaquara*, internal genitalia, dorsal view. Scales: Figs. 1, 2, 4 = 0.5 mm; Figs 3, 5 = 0.25 mm.

1.79, patella and tibia 2.04, metatarsus 1.34, tarsus 0.75. Second patella and tibia 1.42, third 1.2, fourth 1.7.

Variation: Endite apex, distal ends of legs segments, lung plates and base of chelicerae may be red. Dorsal median band and sternum are sometimes totally black, mainly in males. Spermathecae occasionally visible externally. Measurements (mean and standard deviation, $n = 7$): Total length 4.27 ± 0.36 , carapace length 1.37 ± 0.14 , carapace width 1.22 ± 0.08 .

Material examined.—**BRAZIL:** *São Paulo*, Jundiá, Serra do Japi, 13–16 November 1997 (M.O. Gonzaga), 21♀1♂ (IBSP 14403).

Anelosimus jabaquara Levi
(Figs. 4–5)

Anelosimus jabaquara Levi 1956: 414, fig. 18 (Male holotype from Jabaquara, São Paulo, São Paulo, Brazil (H. Sick col.), in American Museum of Natural History, not examined); Levi & Smith 1982: 277 (revalidated).

Anelosimus dubiosus (Keyserling): Levi 1963: 34.

Diagnosis.—Males of *A. jabaquara* can be distinguished from *A. dubiosus* by the short embolus and smaller half-moon tegular process (Levi 1963, fig. 18). The coloration and epigynum of females are similar to that of *A. dubiosus* and *A. jucundus*, from which it can be separated by the structure of the internal genitalia. Like *A. domingo* Levi 1963, this species has broad copulatory ducts, but differs by their lateral insertion on the spermathecae and their trajectory, which covers the fertilization ducts almost completely (Fig. 5).

Description.—**Female:** Coloration as in *A. dubiosus*. Posterior median eyes little more than their diameter apart, slightly less from

laterals. Epigynum a lightly sclerotized, folded plate, with a posterior small projection (Fig. 4). Total length 4.29, carapace 1.79 long and 1.26 wide. First femur 2.24, patella and tibia 2.57, metatarsus 1.9, tarsus 0.89. Second patella and tibia 1.73, third 1.48, fourth 1.9.

Variation: Coloration varies as in *A. dubiosus*. Spermathecae occasionally visible externally. Measurements (mean and standard deviation, $n = 7$): Total length 4.1 ± 0.18 , carapace length 1.62 ± 0.14 , carapace width 1.2 ± 0.07 .

Material examined.—**BRAZIL:** *São Paulo*, Jundiá, Serra do Japi, 13–16 November 1997 (M.O. Gonzaga), 18♀4♂, 2 juv. (IBSP 14404).

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REVISION OF THE *GROENLANDICA* SUBGROUP OF THE GENUS *PARDOSA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. The *groenlandica* subgroup, which currently stands as a component of the *Pardosa modica* group, is characterized by a flat conductor tip in the male palpus and comprises *P. groenlandica* (Thorell 1872), *P. dromaea* (Thorell 1878), *P. bucklei* Kronestedt 1975, *P. tristis* (Thorell 1877), and *P. prosaica* Chamberlin & Ivie 1947. Neotypes are designated to stabilize each of the Thorellian names *iracunda*, *dromaea* and *tristis*, all original material relevant to these names having been lost or destroyed.

Individuals of *Pardosa groenlandica* and related species are among the largest and darkest of the genus *Pardosa* C.L. Koch 1848. Living on exposed mountain slopes and summits, stony beaches or open prairies in North America and Siberia, often in great numbers, they appear to be an integral part of the invertebrate food chains in these habitats (Levi & Levi 1951, 1955; Lowrie & Gertsch 1955; Schmoller 1970; Lowrie 1973; Moring & Stewart 1994). Taxonomic knowledge of these spiders has not kept pace, however, and behaviorists and ecologists have found it impossible to identify their specimens with confidence. This applies particularly to collections from the Cordillera of western North America and the adjacent Great Plains, where populations of two or more of the species apparently occur together and where additional, as yet unknown, species of the subgroup may occur.

Pardosa groenlandica (Thorell 1872), the earliest known species of the assemblage, was originally described from the west coast of Greenland, but the range was later thought to extend across northern Canada to Alaska and the Russian Far East (Dondale & Redner 1990). Three additional species, *P. iracunda* (Thorell 1877), *P. dromaea* (Thorell 1878) (originally described under the name *indagatrix*, which was preoccupied in the genus *Lycosa*) and *P. tristis* (Thorell 1877), had meanwhile been described from Colorado. Thorell thought that his specimens of *iracunda* were extremely similar to and possibly conspecific with those described earlier as *groenlandica*, but he did not resolve the problem. Emerton (1894) examined the type material of *iracun-*

da, *dromaea* and *tristis*, and could find no characters by which to distinguish the three species from *P. groenlandica* or from each other. The type of *P. groenlandica* exists (see below), but those of *P. iracunda*, *P. dromaea* and *P. tristis* then became lost or destroyed, making it impossible for any subsequent workers either to confirm or to refute Emerton's conclusions.

Progress toward a solution began when Kronestedt (1975) published illustrations of the palpus of a male of *P. groenlandica* which he had compared with the types. In the same paper he added a new prairie species, *P. bucklei* Kronestedt 1975, to the assemblage; but he was unable to shed any light on the status of *iracunda*, *dromaea* or *tristis*. Dondale & Redner (1990) determined the probable identity of *P. dromaea* using data on the type locality, body size and female genitalia as given by Thorell (1877) or as illustrated by Emerton (1894). Dondale & Redner (1990) also showed that the range of *P. bucklei* extends into the Cordillera of western North America. The problems posed by the loss of type material and the failure to find diagnostic characters for *P. groenlandica* and related species are addressed in the present paper.

HISTORY OF THE NAMES *IRACUNDA*, *DROMAEA* AND *TRISTIS*

In the summer of 1875 the eminent New England entomologist A.S. Packard, Jr. made a month-long trip to the Front Range of the Rocky Mountains of Colorado and to the Great Salt Lake, Utah to collect arthropods. According to travel information relevant to the time (Holbrook 1947; Bowles 1977),

Packard probably travelled to Cheyenne, Wyoming on the transcontinental Union Pacific Railroad, then southward to Boulder, Colorado on the Cheyenne-Denver Railroad, which had opened in 1870. From the dates given by the identifier of Packard's specimens (Thorell 1877) we can infer that the collector then penetrated the mountainous area west and southwest of Boulder, ascending "Arapaho Peak" (either North Arapaho Peak or South Arapaho Peak), "the Blackhawk" (probably Black Hawk Mountain), "Kelso cabin" (probably a miner's shack on Kelso Mountain) and Grays Peak, with stops for collecting at Golden, "Idaho" (Idaho Springs) and Georgetown. Packard then descended to Denver, where he collected briefly, and proceeded southward, probably using the stagecoach, to "Manitou" (Manitou Springs), "Garden of the Gods" (probably Garden of the Gods Park) and Pikes Peak. His final arachnid collections on the trip were from American Fork Canyon and Great Salt Lake, Utah in late July.

Packard sent his arachnids to Tamerlan Thorell in Sweden. Thorell identified 30 species of spiders, 23 of which he described as new to science (Thorell 1877). There was also a new species of harvestman. Nearly all of the spider material was later returned to Packard, who in turn placed it in the hands of J.H. Emerton. Emerton (1894), in a paper dealing with his own collections from the Lake Louise area of Alberta, mentioned that "Prof. Packard has sent to me the spiders described by Thorell from the Rocky Mountains . . ." Moreover, Emerton provided the first illustrations of any of Thorell's types and, in an addendum to Thorell's paper, described two more species of spiders based on Packard's Colorado material. Today the only known specimens are a male and female of *Pardosa sinistra* (Thorell 1877) (see Kronestedt 1981) and a female of *Pardosa uncata* (Thorell 1877) (see Lowrie & Dondale 1981) in the Swedish Museum of Natural History, Stockholm, perhaps overlooked when Thorell returned the collection to Packard. Enquiries by me at the Swedish Museum of Natural History and the Museo Civico di Storia Naturale "Giacomo Doria" in Genoa (where some of Thorell's types are deposited), at the Peabody Museum of Natural History in Boston (where Packard was custodian for some time) and at the Museum of Comparative Zoology, Har-

vard University (where most of Emerton's collections are now stored) failed to uncover any other relevant types.

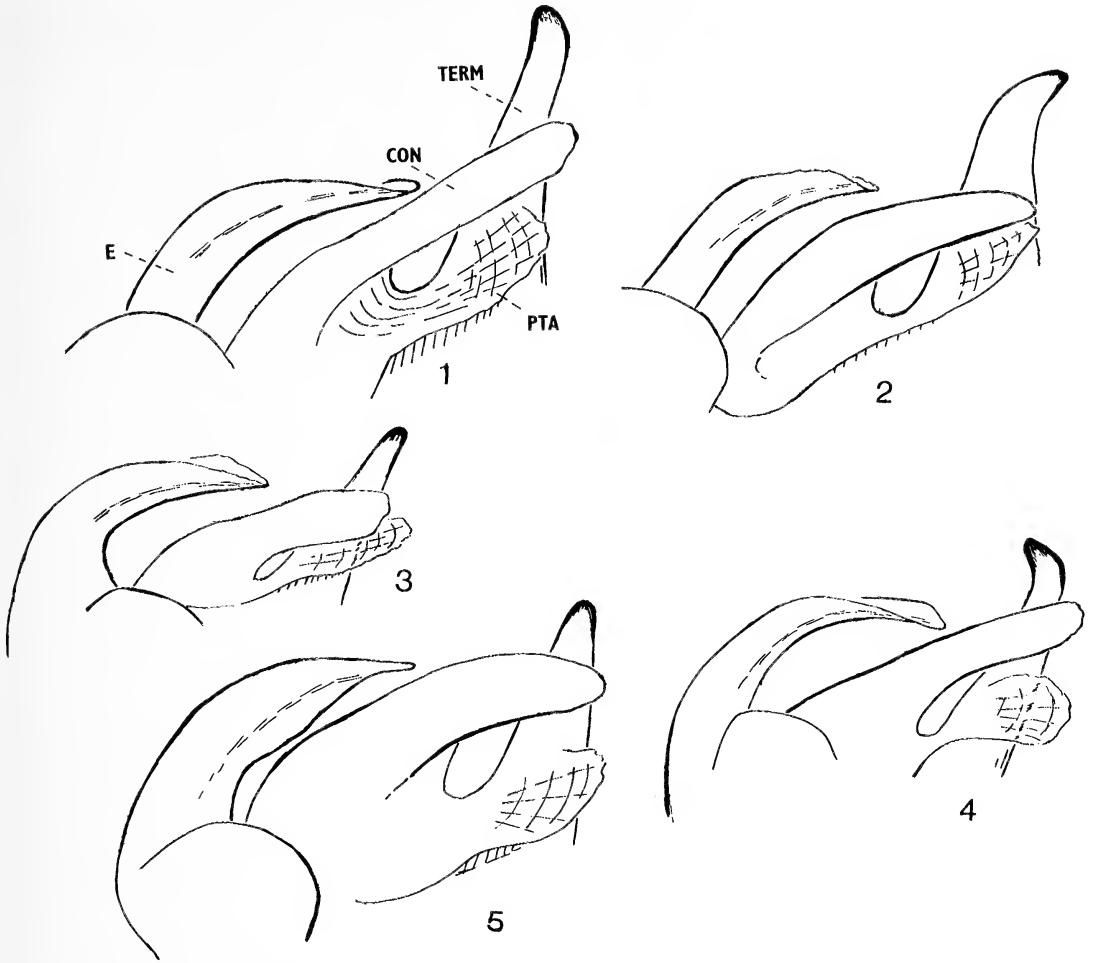
The original description of *Pardosa iracunda* was based on one syntype male from the 13,000 ft. (3965 m) level on Pikes Peak, Colorado and one syntype female from "Kelso Cabin", Colorado. My search, with Jim Redner, of the upper levels of Pikes Peak in 1985 yielded only females, and we never found the locality "Kelso Cabin" on any highway map or gazetteer of Colorado. A male from a mountainous locality near Pikes Peak and deposited in the American Museum of Natural History is selected as neotype of *iracunda* (see below). This specimen fits Thorell's description of *iracunda*.

The holotype female of *P. dromaea* was collected at Denver, Colorado. Because of the difficulty of finding undisturbed habitat in that city, Redner and I concentrated our search along the banks of the South Platte River where it flows through the northern outskirts of the city. A single male specimen, which we judged to be conspecific with females in turn agreeing with Thorell's description of *dromaea*, was found. This male, though of the sex opposite to that of the type, is designated neotype of *dromaea* (permitted by the rules of nomenclature where stability of nomenclature is thereby ensured) (Article 75(d) (4), ICZN).

The original material of *P. tristis* consisted of two syntype females, one from "Idaho" (Idaho Springs), Colorado, the other from "Manitou" (Manitou Springs), Colorado. Our searches at these localities failed to produce specimens that represented any of the species here assigned to the *groenlandica* subgroup, probably because of severe destruction of habitat for road construction in those areas. A specimen from a locality in the same general area as Idaho Springs is therefore selected as neotype of *tristis* (see below). This specimen matches Thorell's description of *tristis*. Courtship and mating behavior observations of *P. groenlandica* were made at various locations in the field.

METHODS

The term retrolateral process of terminal apophysis is used here for a structure of the male palpus (see Figs. 1-5). This structure was illustrated for a male of *P. wasatchensis*



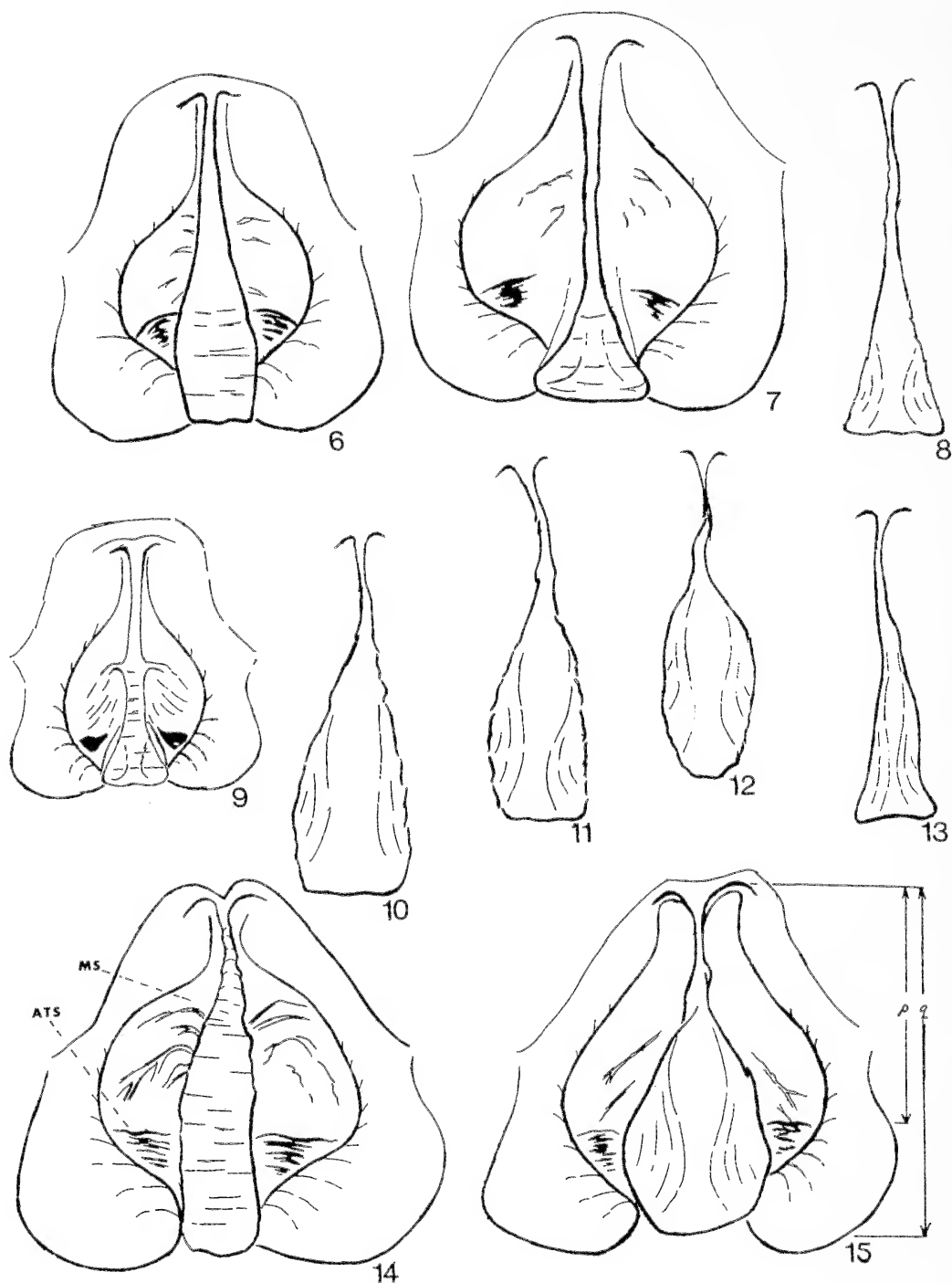
Figures 1–5.—Distal part of male palpus of *Pardosa* spp., retrolaterobasal view. 1, *P. groenlandica*, Sondrestrom Air Base, west Greenland; 2, *P. tristis*, 32 km northwest of Weiser, Idaho; 3, *P. bucklei*, Bear Lake, Utah; 4, *P. dromaea*, Fountain Valley, Colorado; 5, *P. prosaica*, North Fork Pass, Yukon Territory. Abbreviations: CON = conductor, E = embolus, PTA = retrolateral process of terminal apophysis, TERM = terminal apophysis.

Gertsch 1933 by Kronestedt (1993), who called it the retrolateral grooved process of the terminal apophysis. To see this process it is necessary to remove the apical division of the genital bulb (with the embolus, conductor and terminal apophysis intact) from the tegulum (see Dondale & Redner 1990 for definitions of terms). If the preparation is viewed prolaterobasally, the retrolateral process of terminal apophysis is seen as a tooth, ridge or similar structure on the side of the terminal apophysis near its base.

A second character used frequently in this work is the epigynal ratio. This is calculated

from $p/q \times 100$, where p is the distance from the anterior end of the median septum to the anterior margins of the atrial sclerites, and q is the total length of the median septum (Fig. 15). Differences in the means of epigynal ratios are compared using an ANOVA.

The following abbreviations are used for museums: AMNH (American Museum of Natural History, New York, New York); CNC (Canadian National Collection of Insects and Arachnids, Ottawa, Ontario); MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts); NRS (Swedish Museum of Natural History, Stock-



Figures 6-15.—Female genitalia of *Pardosa* spp., ventral view. 6, 7, 9, 14, 15, Epigynum; 8, 10-13, Median septum. 6, *P. dromaea*, Woolford Provincial Park, Alberta; 7, *P. tristis*, Salmon Arm, British Columbia; 8, *P. tristis*, Penticton, British Columbia; 9, *P. bucklei*, Mormon Lake, Arizona; 10, 11, *P. prosaica*, Magadan area, Russia; 12, *P. prosaica*, Hyndman Lake, Northwest Territories; 13, *P. prosaica*, East Chukotka Peninsula, Russia; 14, *P. groenlandica*, Sondrestrom Air Base, west Greenland; 15, *P. prosaica*, Old Crow, Yukon Territory. Abbreviations: ATS = atrial sclerite, MS = median septum, p = distance from anterior end of median septum to anterior margin of atrial sclerite, q = length of median septum.

holm, Sweden); IBPN (Institute for Study of Biological Problems of the North, Magadan, Russia).

RELATIONSHIPS

Dissections of male palpi indicate that a retrolateral process of terminal apophysis is present in males of most members of the *Pardosa modica* group, of which the *groenlandica* subgroup is a component (for current composition of the *modica* group see Kronestedt 1975, 1981, 1986, 1988, 1993 and Dondale & Redner 1990). The retrolateral process of terminal apophysis is apparently absent in male *P. modica* (Blackwall 1846), and it apparently occurs in males of at least a few species in other groups of the genus *Pardosa*.

In males of two lineages of *modica*-group species the retrolateral process of terminal apophysis occupies much of the space between the base of the terminal apophysis and the free part of the conductor (Figs. 1–5). This expression of the process, called “large,” is restricted, in the first place, to males of *P. groenlandica*, *P. dromaea*, *P. bucklei*, *P. tristis* and *P. prosaica*. Males of all five of these species are characterized by the unique possession of a flat conductor tip (Figs. 1–5). Together these species comprise the *groenlandica* subgroup. The second lineage in which the males have a large retrolateral process of terminal apophysis comprises *P. wasatchensis* Gertsch 1933, and some related species that are the subject of a future investigation.

Within the *groenlandica* subgroup one can discern two further lineages based on the shape of the retrolateral process of terminal apophysis. In males of *P. groenlandica* and *P. dromaea* this structure is a thin upright ridge that arises angularly from the free part of the conductor (Figs. 1, 4). Males of *P. bucklei*, *P. tristis* and *P. prosaica*, on the other hand, have a retrolateral process of terminal apophysis with a long low margin (Figs. 2, 3, 5).

SYSTEMATICS

Pardosa groenlandica (Thorell)

Figs. 1, 14, 16

Lycosa groenlandica Thorell 1872: 157. Syntype male from Disko Island, West Greenland (69°15'N, 3°32'W (Th. Fries), deposited in NRS (Thorell Collection No. 244/1524a), examined and here designated LECTOTYPE. Syntype female from the type locality, 3 July 1871, depos-

ited in NRS, examined and here designated PAR-ALECTOTYPE.

Lycosa iracunda Thorell 1877: 514. Syntype male from Pikes Peak (38°50'N, 105°02'W), 3965 m elevation, El Paso County, Colorado, 14 July 1875 (A.S. Packard, Jr.), and syntype female from ‘Kelso Cabin’ (probably on Kelso Mountain, 39°33'N, 105°47'W), Clear Creek County, Colorado, 6 July 1875 (A.S. Packard, Jr.), both lost or destroyed. NEOTYPE male from Pikes Peak, 3660 m elevation, El Paso County, Colorado, 24 June 1940 (W.J. Gertsch and L. Hook), deposited in AMNH, here designated. Name *iracunda* first synonymized under *groenlandica* by Emerton (1894: 423), here confirmed.

Pardosa groenlandica: Emerton 1894: 423(part); Kronestedt 1975: 218, figs. 3c, 4C, 4c; Dondale & Redner 1990: 212, figs. 300–304.

Diagnosis.—Males of *P. groenlandica* are distinguished from males of other species of *Pardosa* except *P. dromaea* by the possession of a ridgelike retrolateral process of terminal apophysis, the margin of which is angular (Fig. 1). I have not found a character in the male palpus by which to distinguish males of *P. groenlandica* from those of *P. dromaea*, but the former males are significantly larger (Table 1), and they court by approaching females after drumming their bodies on the substrate (rather than while drumming). In addition, individuals of *P. groenlandica* range in the western North American Cordillera, in northern and eastern Canada and in Greenland (rather than the Central Plains), and they occupy stony or gravelly habitats (rather than prairie habitats). Females of *P. groenlandica* differ from those of other species of *Pardosa* except *P. dromaea* in the shape of the median septum: this structure widens in the posterior two-thirds or three-fourths and is parallel or somewhat convex at the lateral margins (Fig. 14). Females of *P. groenlandica* are significantly larger than those of *P. dromaea* (and those of *P. bucklei*) (Table 1), and the range and habitats differ as stated for males. The epigynal ratio of 71.1 ± 4.6 (Colorado sample) is significantly larger ($P < 0.05$) than that of *P. dromaea* (Table 2).

Description.—*Male*: Carapace black to dark reddish-brown, with pale median area, and with lateral bands represented by three or four yellowish spots. Legs black to reddish-brown, distally yellowish; femora, tibiae, and basitarsi often with broad pale rings. Abdomen dull black, usually mottled with dull red,

Table 1.—Measurements (in mm) of *Pardosa groenlandica*, *P. dromaea*, *P. bucklei*, *P. tristis* and *P. prosaica*. Sample size is 20 individuals of each sex. Data for *P. bucklei* are from Dondale & Redner (1990). Means significantly different within columns bear same superscript.

Species	Total length		Carapace length		Carapace width	
	Male	Female	Male	Female	Male	Female
<i>Groenlandica</i>	8.68 ± 0.60 ^{ab}	9.42 ± 1.19 ^{ab}	4.26 ± 0.25 ^{ab}	4.30 ± 0.41 ^{ab}	3.32 ± 0.23 ^{abc}	3.41 ± 0.36 ^{abc}
<i>Dromaea</i>	7.80 ± 0.43 ^{acg}	8.60 ± 0.98 ^{acdh}	4.00 ± 0.25 ^{acdei}	3.86 ± 0.42 ^{acdh}	2.98 ± 0.21 ^{adi}	2.95 ± 0.35 ^{adej}
<i>Bucklei</i>	6.86 ± 0.70 ^{bcd}	7.86 ± 1.03 ^{bcefg}	3.47 ± 0.34 ^{bcefg}	3.56 ± 0.27 ^{bcefg}	2.55 ± 0.26 ^{bdeh}	2.67 ± 0.28 ^{bdfgi}
<i>Tristis</i>	8.67 ± 0.79 ^d	9.41 ± 0.87 ^{de}	4.22 ± 0.33 ^{def}	4.22 ± 0.27 ^{de}	3.25 ± 0.25 ^{eg}	3.29 ± 0.29 ^{efh}
<i>Prosaica</i>	9.07 ± 0.62 ^{efg}	9.43 ± 0.61 ^{fg}	4.32 ± 0.40 ^{ghi}	4.42 ± 0.37 ^{gh}	3.49 ± 0.28 ^{cfghi}	3.66 ± 0.27 ^{efghj}

and with reddish heart mark. Palpus (Fig. 1) dark, hairy; tegulum protruding at base; median apophysis small, with basal process slender and sinuous; embolus broad at base, more slender distally, usually with inconspicuous flange at tip; terminal apophysis stout, curved, with tip straight or deflected basally (retrolateral view); conductor broad, flat; retrolateral process of terminal apophysis large, ridgelike, with margin abruptly angular. Measurements: see Table 1.

Female: Coloration essentially as in male, but pale areas of carapace more distinct and legs paler. Epigynum (Fig. 14) with flask-shaped atrium; median septum slender anteriorly, distinctly wider in posterior two-thirds or three-fourths, with lateral margins somewhat angular, usually parallel or somewhat convex; atrial sclerites broad, prominent; epigynal ratio: see Table 2, and Biology for variation; spermathecae long, club-shaped, with several nodules (Dondale & Redner 1990, fig. 304). Measurements: see Table 1.

Material examined.—There are 433 adult specimens, all bearing my label, deposited as VOUCHERS in the following institutions: AMNH (116♂133♀); CNC (33♂34♀, including those from courtship studies); MCZ (6♂3♀).

Range.—Western Northwest Territories to Greenland, south to the Great Lakes and the coast of Maine, and, in the Rocky Mountains, to northern Utah and central Colorado (Fig. 16).

Biology.—Adults of *P. groenlandica* have been collected from mid-May to early September; the late-season individuals were all females. Schmoller (1970), whose voucher specimens of *P. tristis* I examined in the American Museum of Natural History, represent *P. groenlandica* as defined here. He studied an alpine population on Mount Evans and on the upper levels of Rocky Mountain National Park. His examination of size distributions in specimens collected on successive dates through the summer led Schmoller to infer a biennial life history in those areas. He also observed mating in July, and the presence of egg sacs from late July to September. Newly emerged spiderlings attained a pre-wintering length of about 5.75 mm, and grew to the penultimate stage during the following summer. These individuals then matured the subsequent June, approximately 23 months after

Table 2.—Genitalic characters of specimens of *Pardosa groenlandica*, *P. dromaea*, *P. bucklei*, *P. tristis* and *P. prosaica*. In column “Epigynal ratio”, significant differences between means are indicated by same letter.

Species	Embolus	Retrolateral process of terminal apophysis	Median septum	Epigynal ratio
<i>Groenlandica</i>	Slender, with terminal flange	Ridgelike, angular	Widening in posterior two-thirds or three-fourths, with margins parallel or convex	71.1 ± 4.6 ^a (Colorado sample)
<i>Dromaea</i>	Slender, with terminal flange	Ridgelike, angular	Widening in posterior two-thirds or three-fourths, with margins parallel or convex	67.9 ± 4.0 ^{abc}
<i>Bucklei</i>	Broad, truncate	Low	Slender, abruptly widening at posterior end	72.6 ± 4.0 ^b (Utah sample)
<i>Tristis</i>	Slender, with terminal flange	Low	Slender, gradually widening in posterior half	71.7 ± 3.1 ^c
<i>Prosaica</i>	Thickened near middle, with pointed tip	Low	Slender anteriorly, widening in posterior three-fourths to two-thirds	70.3 ± 4.9

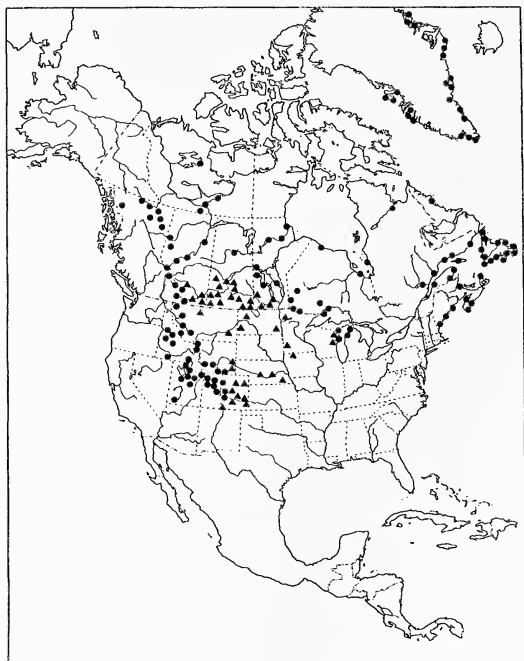


Figure 16.—Collection localities of *Pardosa groenlandica* (●, circles) and *P. dromaea* (▲, triangles).

they hatched. It is possible that Schmoller included specimens of *P. tristis* in his work, as specimens of both that species and of *P. groenlandica* are now known to occur on Mount Evans. Repetition of his work is needed on known specimens. The same applies to an excellent study of *P. groenlandica* on a pebbly beach at Flathead Lake, Montana (Ricards 1967), where populations of *P. tristis* and of *P. bucklei* occur together with one of *P. groenlandica*.

Courtship by males of *P. groenlandica* has been observed some 29 times by J.H. Redner and/or myself at localities on the Atlantic coast of Canada, at Bagotville, Quebec and in Colorado. On detecting a female, the male always ceased moving for a time, drawing his body close to the substrate and extending his legs I stiffly forward. The body was then raised while the palpi were held forward and downward. While in this posture, the male began to move his palpi in small circles a little above the substrate. The right palpus circled clockwise and the left one counterclockwise. Three or four circles was the usual number, both palpi moving at the same time. Then one palpus or the other was raised quickly to an

angle of approximately 80° with the substrate, held aloft for an instant, and quickly lowered to the resting position. Both palpi then resumed circular motions for a second or two, after which the alternate palpus was raised, held, and lowered as the first had been. This sequence was repeated several times while the spider remained at one spot.

After a number of such palpal sequences, the male suddenly raised his body to maximum height, then lowered it in a rapid series of four or five taps against the substrate so that at the end of the series his body lay flat against the substrate and his legs were held outspread. The tapping series was accompanied by a rapid vibration of legs I, usually alternately but occasionally in unison; this leg action produced an audible rattle. At completion of the tapping series, the male moved at moderate speed toward the female, his legs vibrating audibly on the substrate. This forward dash was usually interrupted one or more times by a resumption of palpal circling. Eventually the male was close enough to the female to vibrate his legs on her body and legs, and to mount and copulate. Courtship lasted about 15 minutes.

In a typical mating the male inserted his right or left embolus into the corresponding copulatory tube of the female as follows: 1 insertion on left side, 1 on right, 2 on left, 1 on right, 1 on left, 1 on right, 1 on left, 2 on right, 1 on left, 1 on right, 1 on left, 2 on right, 1 on left, 1 on right, 1 on left. Each insertion was accompanied by one to five brief pulsations of the palpal haematodocha and each pulsation was followed by a brief partial deflation of that organ.

The epigynal ratio of *P. groenlandica* appears to vary geographically. This ratio was calculated for 16 females from each of seven parts of the range, with the following results: Utah (68.5 ± 5.8); Colorado (71.1 ± 4.6); Wyoming (73.5 ± 3.6); Montana (71.9 ± 4.8); Alberta/Northwest Territories (69.2 ± 5.2); Greenland (68.9 ± 4.3); Atlantic Provinces of Canada (66.6 ± 3.4).

The sample mean for the Atlantic Provinces is smaller than means for the other six areas. This difference is statistically significant for the samples from Colorado ($P < 0.01$), Montana ($P < 0.01$) and Wyoming ($P < 0.01$), and approaches the 5% level of significance for Alberta/Northwest Territories ($P < 0.09$). I in-

fer that the population living on the Atlantic coast, which is somewhat isolated from the others, has developed small but measurable differences. I have not found a corresponding difference in the palpi of Atlantic coast males.

A second point to note from the value for epigynal ratio is that the Wyoming sample, which gives the largest mean, is statistically different from those from Utah ($P < 0.01$), Alberta/Northwest Territories ($P < 0.05$), Greenland ($P < 0.01$) and the Atlantic coast ($P < 0.01$), and approaches that level for the Montana ($P < 0.08$) and Colorado ($P < 0.08$) samples. This Wyoming population seems to invite further investigation, but was not so treated in this study. The mean epigynal ratio did not differ significantly between any pair of samples from Utah, Colorado, Montana, Alberta/Northwest Territories or Greenland.

In the southern parts of the range of *P. groenlandica*, individuals occur on alpine tundra or among bare rocks at or above timber line. On the Atlantic coast, however, populations thrive on pebbly or cobblestone beaches at or somewhat above sea level.

Pardosa dromaea (Thorell)

Figs. 4, 6, 16

Lycosa indagatrix Thorell 1877: 512. Holotype ♀ from Denver (39°44'N, 104°59'W), Denver County, Colorado, 10 July 1875 (A.S. Packard, Jr.), lost or destroyed. NEOTYPE male from South Platte River at 88th Street, Denver, Denver County, Colorado, 20 June 1985 (C.D. Dondale & J.H. Redner), here designated, deposited in CNC. Name *indagatrix* preoccupied in genus *Lycosa*.

Lycosa dromaea Thorell 1878: 395. New name for *Lycosa indagatrix*, preoccupied.

Pardosa groenlandica: Emerton 1894: 423, fig. 1b (pl. 4). Holotype female of *P. indagatrix* illustrated.

Pardosa nebraska Chamberlin & Ivie 1942: 30, figs. 69, 70 (pl. 7). Holotype ♂ from 6 km west of Lexington (40°50'N, 99°55'W), Dawson County, Nebraska, 6 June 1933 (W. Ivie), deposited in AMNH, examined. Name *nebraska* first synonymized by Dondale & Redner (1990).

Pardosa dromaea: Simon 1898: 359; Dondale & Redner 1990: 209, figs. 305–307.

Diagnosis.—Males of *P. dromaea* are distinguished from those of other species of *Pardosa* except *P. groenlandica* by the possession of a ridgelike retrolateral process of terminal apophysis, the margin of which is an-

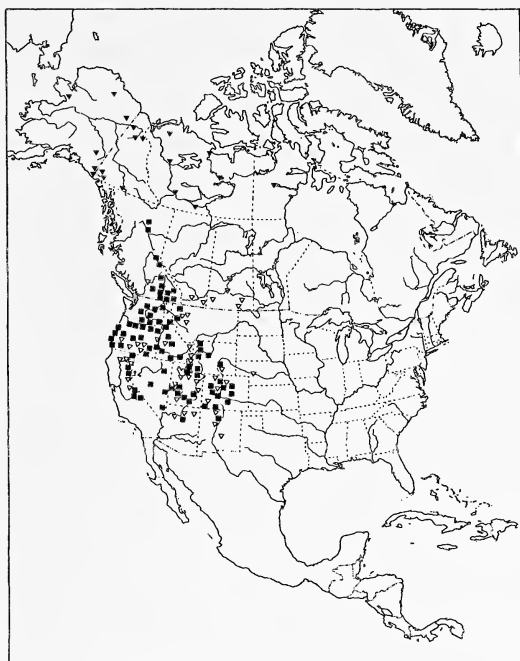


Figure 17.—North American collection localities of *Pardosa prosaica* (▼, solid triangles), *P. bucklei* (▽, hollow triangles) and *P. tristis* (■, squares).

gular (Fig. 4). Males are significantly smaller than those of *P. groenlandica* (Table 1), and they tap their bodies on the substrate while dashing toward the female rather than tapping while remaining stationary. They also occur in prairie habitats on the Central Plains rather than in the Cordillera and the northern parts of the North American continent. Females of *P. dromaea* differ from those of other species of *Pardosa* except *P. groenlandica* in possessing a median septum that widens in the posterior two-thirds or three-fourths and has parallel or convex lateral margins (Fig. 6). Females of *P. dromaea* are significantly smaller than those of *P. groenlandica* and significantly larger than females of *P. bucklei* (Table 1), and differ in range from the former (see Figs. 16, 17). The epigynal ratio of 67.9 ± 4.0 is significantly smaller ($P < 0.05$) than that of *P. groenlandica* (Colorado sample), *P. bucklei* ($P < 0.01$), and *P. tristis* ($P < 0.01$) (Table 2).

Description.—*Male*: Carapace black to dark reddish-brown, with median band often reduced to a small spot, and with submarginal bands represented by three or four small yellowish spots. Legs black to dark reddish-

brown, often with darker rings on femora and tibiae. Abdomen black dorsally, mottled with dull red, with pale heart mark; venter reddish-brown to yellowish. Palpus (Fig. 4) dark, hairy; tegulum protruding at base; median apophysis small, with slender sinuous basal process; embolus broad at base, with small flange at tip; terminal apophysis toothlike, curved, with tip straight or deflected somewhat basad (retrolaterobasal view, Fig. 4); conductor broad, flat; retrolateral process of terminal apophysis large, ridgelike, with angular margin. Measurements: see Table 1.

Female: Coloration essentially as in male, but legs somewhat paler. Epigynum (Fig. 6) with flask-shaped atrium; median septum slender anteriorly, broader in posterior two-thirds or three-fourths, with lateral margins parallel or convex; atrial sclerites broad, prominent; epigynal ratio: see Table 2; spermathecae long, curved, club-shaped, with small nodules (Dondale & Redner 1990, fig. 307). Measurements: see Table 1.

Material examined.—There are 244 adult specimens, all bearing my label, deposited as VOUCHERS in the following institutions: AMNH (37♂46♀); CNC (88♂89♀); MCZ (3♂1♀); A pair of VOUCHER specimens from Moring & Stewart's (1994) study in Colorado is deposited in CNC.

Range.—Eastern foothills of the Rocky Mountains in Alberta, Montana, Wyoming, Colorado and New Mexico, east to southern Manitoba, Minnesota, Iowa and Nebraska (Fig. 16). The species is regarded as a member of the Great Plains fauna.

Biology.—Specimens of *P. dromaea* have been collected from late April to early September. I have observed male courtship only twice, but Donald J. Buckle (pers. comm.) has observed it many times. The specimens were respectively from the Lethbridge, Alberta area and from Saskatoon, Saskatchewan. The sequence of palpal and leg movements appeared to be like that of male *P. groenlandica* (see above), but the body tapped the substrate while the male dashed toward the female rather than while stationary. Courtship lasted approximately 20 minutes, copulation 25–30 minutes. The insertion series in one mating was as follows: 2 insertions on right side, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left. Each

insertion was accompanied by 1–8 brief pulsations of the haematodocha.

An ecological study was recently published on *P. dromaea* (reported as *P. tristis*) by Moring & Stewart (1994). The principal habitats of *P. dromaea* along the Conejos River in south-central Colorado were reported as rock-cobble, grass-willow, and sand-cobble. Leaf litter near the river produced no specimens of *P. dromaea*.

Pardosa bucklei Kronestedt

Figs. 3, 9, 17

Pardosa bucklei Kronestedt 1975: 224, figs. 2c, 3d, 4D, 4d, 6c, 6e, 7c, 9. Holotype male from 17 miles (27 km) west of Saskatoon (52°07'N, 106°38'W), Saskatchewan, 18 July 1965 (D.J. Buckle), deposited in CNC, examined; Dondale & Redner 1990: 205, figs. 292–295.

Diagnosis.—Males of *P. bucklei* are distinguished from those of other species of *Pardosa* by the broad truncate embolus (Dondale & Redner 1990, figs. 292, 293). They uniquely share with males of *P. tristis* and *P. prosaica* a low margin of the retrolateral process of terminal apophysis (Fig. 3 & Table 2). Females are distinguished by the slender median septum, which widens abruptly at the posterior end (Fig. 9); the epigynum closely resembles that of *P. lowriei* Kronestedt 1975, but is much smaller, as are the body dimensions. Individuals of *P. bucklei* are the smallest among those assigned to the *groenlandica* subgroup (Table 1). The mean epigynal ratio of *P. bucklei* is significantly larger than that of *P. dromaea*, but not of *P. groenlandica*, *P. tristis* or *P. prosaica* (Table 2). The epigynal ratio of 72.6 ± 4.0 (Utah sample) is significantly larger than that for *P. dromaea* ($P < 0.01$).

Description.—**Male:** Carapace dark reddish-brown, with distinct pale median band, and with submarginal bands reduced to three or four yellowish spots. Legs yellowish, darkest at base on dorsal side, with indistinct darker rings on femora and tibiae. Abdomen grayish, with series of pale chevrons or triangles along midline; heart mark pale; venter pale gray. Palpus (Fig. 3) dull yellowish, hairy; median apophysis small, situated in cavity of tegulum, with basal tooth slender and sinuous; embolus broad, flat, truncate; terminal apophysis toothlike, curved, deflected anteriorly at tip (retrolaterobasal view, Fig. 3); conductor broad, flat at tip, with margins somewhat de-

flected; retrolateral process of terminal apophysis large, weakly sclerotized, with low margin. Measurements: see Table 1.

Female: Coloration essentially as in male, but legs much paler and abdomen paler and less hairy. Epigynum (Fig. 9) with flask-shaped atrium; median septum slender throughout most of its length, abruptly widened at posterior end; atrial sclerites small, distinct, variable in width, continuous anteromedially with one or more of the low ridges extending from sides of median septum; epigynal ratio: see Table 2; spermathecae club-shaped (Dondale & Redner 1990, fig. 295). Measurements: see Table 1.

Material examined.—There are 235 adult specimens, all bearing my label and deposited in the following institutions: AMNH (53♂174♀); CNC (4♂6♀).

Range.—Southern interior of British Columbia, east to central Saskatchewan and Nebraska, south to the northern interior of California, northern Arizona and northern and central New Mexico (Fig. 17).

Biology.—Adults have been collected from mid-April to early September. Prairie specimens were observed at the margins of sloughs and saline lakes, and Cordilleran specimens at the margins of lakes, streams or reservoirs. A few originated in fields of clover or alfalfa, or in sagebrush.

Two samples of 16 females each, one from prairie localities and the other from the Uintah and Sawatch Mountains in Utah, had respectively epigynal ratios of 74.1 ± 4.0 and 72.6 ± 4.0 . The difference between these means is not statistically significant.

Pardosa tristis (Thorell)

Figs. 2, 7, 8, 17

Lycosa tristis Thorell 1877: 510. Syntype female from "Idaho" (Idaho Springs, 39°44'N, 105°00'W), Clear Creek County, Colorado, 5 July 1875 (A.S. Packard, Jr.), and syntype female from Williams Canyon, "Manitou" (Manitou Springs, 38°51'N, 104°55'W), El Paso County, Colorado, 17 July 1875 (A.S. Packard, Jr.), both lost or destroyed. NEOTYPE female from Mt. Evans, 14,000 feet (4300 m) elevation (39°35'N, 105°38'W), Clear Creek County, Colorado, 25 July 1961 (B.H. Poole), deposited in CNC.

Pardosa groenlandica: Emerton 1894: 423 (part).

Pardosa tristis: Banks 1895: 430 (part).

Diagnosis.—Males of *P. tristis* are distin-

guished from those of other species of *Pardosa* except *P. bucklei* and *P. prosaica* by the low margin of the retrolateral process of terminal apophysis (Fig. 2). They are significantly larger than those of *P. dromaea* and of *P. bucklei* (all three dimensions) and significantly smaller than those of *P. prosaica* in carapace width (Table 1). Females of *P. tristis* differ from those of other species of *Pardosa* by the shape of the median septum, which gradually widens in the posterior half and has the lateral margins concave (Figs. 7, 8). Females are significantly larger than those of *P. dromaea* and *P. bucklei*, but significantly smaller than females of *P. prosaica* in carapace width (Table 1). The epigynal ratio of 71.7 ± 3.1 is significantly larger than that of *P. dromaea* ($P < 0.01$) (Table 2). The range of *P. tristis* overlaps that of *P. groenlandica* and *P. bucklei* but not, apparently, that of *P. dromaea* or *P. prosaica*.

Description.—**Male:** Carapace black to dark reddish-brown, with small pale median band and with lateral bands represented by three or four small yellowish spots. Legs black basally, yellowish distally, with broad dark rings on femora and tibiae. Abdomen black dorsally, with reddish heart mark; venter gray or dull yellow. Palpus (Fig. 2) black, hairy; tegulum strongly protruding at base; median apophysis small, situated in cavity of tegulum, with slender sinuous basal process; embolus broad at base, tapered and straight distally, usually with small flange at tip; terminal apophysis toothlike, curved; conductor broad, flat, with tip somewhat curved; retrolateral process of terminal apophysis large, weakly sclerotized, with low margin. Measurements: see Table 1.

Female: Coloration essentially as in male, but legs (and sometimes abdominal dorsum) more grayish. Epigynum (Figs. 7, 8) with flask-shaped atrium; median septum slender anteriorly, gradually widened in posterior half, usually with lateral margins concave; atrial sclerites small, distinct, usually restricted to lateral two-thirds of atrium; epigynal ratio: see Table 2; spermathecae club-shaped, with small nodules distally, like spermathecae of *P. groenlandica* and *P. dromaea*. Measurements: see Table 1.

Material examined.—There are 1098 adult specimens, all bearing my label, deposited as

VOUCHERS in the following institutions: AMNH (189♂466♀); CNC (68♂85♀); MCZ (143♂159♀).

Range.—Interior British Columbia to the northern interior of California, east to western Montana, the Rocky Mountain Front Range of Colorado and northern New Mexico (Fig. 17).

Biology.—Adults of *P. tristis* have been collected from the end of March to mid-September. One male in the collections was found in a human dwelling in February at Moscow, Idaho. Individuals of *P. tristis* are often found in vegetated canyons and gullies at elevations up to 3000 m. Such habitats are widespread in the Great Basin and the Columbia Plateau.

Specimens of *P. tristis* from sand dunes and beaches along the coast of Oregon tend to be much paler than inland specimens; the carapace, abdomen and legs are almost entirely unmarked, with only traces of dark pigment in most specimens. A sample of 16 of these pale *P. tristis* in the collections of the American Museum of Natural History does not differ significantly in carapace dimensions from a similar sample taken in the Oregon interior. The mean epigynal ratio of 16 of the pale specimens also does not differ significantly from that of 16 specimens from interior Oregon.

Pardosa prosaica Chamberlin & Ivie
Figs. 5, 10–13, 15, 17

Pardosa prosaica Chamberlin & Ivie 1947: 21, fig. 89 (pl. 10). Holotype female from Quartz Creek, 15–16 miles (approximately 24 km) north of Haycock (65°13'N, 161°10'W), Seward Peninsula, Alaska, 11 August 1946 (R.D. Hamilton), deposited in AMNH, examined. Dondale et al. 1997: 96.

Pardosa groenlandica: Kronstedt 1986: 215; Dondale & Redner 1990: 212, figs. 300–304 (in part); Marusik et al. 1992: 149; Marusik et al. 1993: 75; Bartosh & Gorbunova 1994: 119, figs. 1–3, 10.

Diagnosis.—Males of *P. prosaica* are distinguished from those of other species of *Pardosa* by the embolus, which is conspicuously widened near the middle and pointed at the tip (Fig. 5). The retrolateral process of terminal apophysis is like that of *P. bucklei* and *P. tristis*. Females are distinguished by the median septum, which is extremely slender anteriorly but abruptly and often conspicuously widened in the posterior three-fourths to two-thirds (Figs. 10–13, 15). Individuals of *P.*

prosaica are the largest (Table 1) and darkest of the members of the *groenlandica* subgroup. I have found no significant differences between the available Asian specimens and North American specimens. The range of *P. prosaica*, based on current knowledge, overlaps that of only *P. groenlandica* among the members of this subgroup.

Description.—*Male*: Carapace black to dark reddish-brown, with pale median and lateral bands reduced to a trace, sometimes absent. Legs black to dark reddish-brown; femora, tibiae and basitarsi with broad, faintly indicated paler rings. Abdomen dull black, with faintly indicated heart mark. Palpus (Fig. 5) black, hairy; tegulum protruding at base; median apophysis small, with basal process slender, sinuous; embolus long, flat, conspicuously widened near middle, pointed at tip, lacking flange; terminal apophysis stout, curved, with tip straight (retrolaterobasal view); conductor broad, curved, with tip flat; retrolateral process of terminal apophysis large, with low margin (Fig. 5). Measurements: see Table 1.

Female: Coloration much as in male, but pale median band and lateral spots usually distinct, and heart mark often visible. Epigynum (Figs. 10–13, 15) with flask-shaped atrium; median septum flat, extremely slender anteriorly, abruptly widening and usually conspicuously wide in posterior three-fourths to two-thirds, convex or truncate at posterior end; atrial sclerites broad, prominent; epigynal ratio: see Table 2; spermathecae long, club-shaped, with several nodules (Bartosh & Gorbunova 1994) Measurements: see Table 1.

Material examined.—Ninety adult specimens, including Asian specimens as follows: **RUSSIA**: East Chukotka Peninsula, Bolshaya Osinovaya River (tributary of Belaya River): 5♀; Northeast Siberia, Magadan area, Ola River: 1♂2♀. All of these bear my label and are deposited as VOUCHERS in the following institutions: AMNH (9♂29♀); CNC (20♂74♀); IBPN (1♂7♀).

Range.—Alaska, Yukon Territory, and western Northwest Territories (Fig. 17); middle and eastern Asia. *Pardosa prosaica* is regarded as part of the Subarctic/Alpine fauna (Dondale et al. 1997).

Biology.—Dates of collection range from early June to late July. Specimens of *P. prosaica* have been collected in stony creek beds,

in rock slides or plant debris along river banks and on bogs and alpine tundra.

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A REVISION OF CENTRAL AFRICAN *TRABEA* (ARANEAE, LYCOSIDAE) WITH THE DESCRIPTION OF TWO NEW SPECIES FROM MALAWI AND A REDESCRIPTION OF *T. PURCELLI*

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ABSTRACT. The central African representatives of the genus *Trabea* are revised. *Trabea straeleni* (Roewer 1960) is revalidated as a good species and redescribed. *Trabea heteroculata* Strand 1913 is redescribed, and two new species from Malawi are added: *Trabea nigristernis* new species and *Trabea setula* new species. For comparison, a related southern African species, *Trabea purcelli* Roewer 1951, is redescribed. Some notes on the southern African *Trabea ornatipalpis* Russell-Smith 1982 are given together with a short zoogeographical discussion of the genus *Trabea* as a whole.

Simon (1876) created the genus *Trabea* for the Mediterranean species *paradoxa* (note correct spelling, not *Trabaea*; cf. Roewer 1954; Platnick 1989, 1993). The genus was revised by Russell-Smith (1982) to whose paper I refer for discussions at the generic and subfamilial level and for a diagnosis of the genus. Nine valid species were retained within *Trabea* at that time, eight from sub-Saharan Africa and one from the Mediterranean region. Snazell (1983) discovered a tenth species in southern Spain, which he named *cazorla*. This species was later also recorded from northern Spain (Barrientos 1985) and northern Africa (Alderweireldt et al. 1992).

From central Africa, two species were known. *Trabea straeleni* (Roewer 1960, sub *Trabaeosa*) was described from Congo (Zaire) but synonymized by Russell-Smith (1982) with the South African *T. purcelli* (Roewer 1951, sub *Trabaeosa*). The study of further material indicates that this synonymy, which was based on female material only, was incorrect. Therefore *T. straeleni* is revalidated here. Besides this, *T. heteroculata* Strand 1913 is known from Ruanda and Tanzania. While studying a spider collection from Malawi (deposited in the Royal Museum of Central Africa, Tervuren, Belgium), two new species of *Trabea* were discovered. They are described here within the framework of a revision of all known central African species. Besides this, further records are added to the distribution of both *T. straeleni* and *T. heteroculata*.

Abbreviations used in the text are as follows: MRAC = Royal Museum of Central Africa (R. Jocqué), NHRS = Swedish Museum of Natural History (T. Kronstedt), PCMA = Private collection M. Alderweireldt, SAM = South African Museum (M.A. Cochrane), SMF = Senckenberg Museum Frankfurt (M. Grasshoff), ZMB = Zoological Museum Berlin (Sh. Nawai), CW = carapace width in mm, CL = carapace length in mm, TL = total length in mm. All measurements indicate mean value with range between brackets.

TAXONOMY

Trabea Simon 1876: 357. Type species
Trabea paradoxa Simon by monotypy.

Trabea: Russell-Smith 1982: 70.

Trabea straeleni (Roewer 1960) (revalidated)
Figs. 1–3

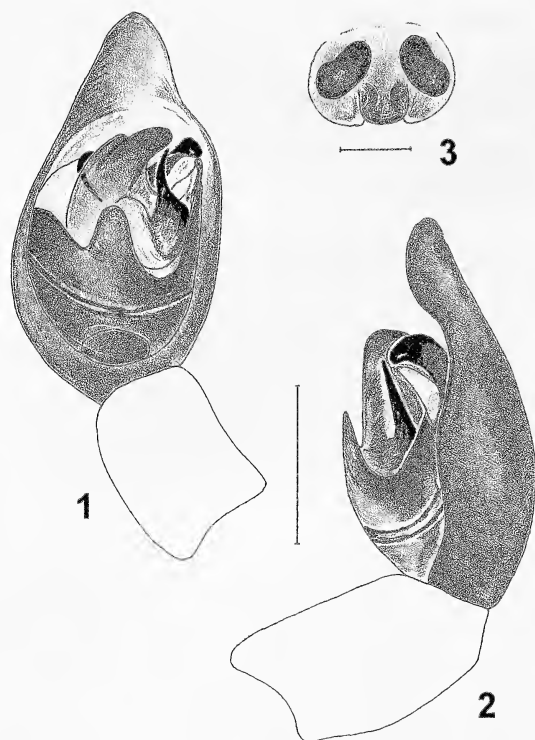
Trabaeosa straeleni Roewer 1960: 585, fig. 331.

Trabaea straeleni: Russell-Smith 1982: 74, fig. 3,
fig. 11D (sub *T. purcelli*)

Pseudevippa bipunctata Roewer 1959: 204, fig.
107; Alderweireldt 1991: 379 (see remark under
T. purcelli)

Type material.—**CONGO (ZAIRE):** Lusinga hill, 1810 m, 16 July 1947, 1 ♀ holotype, (Mission De Witte) (MRAC 139.442) (examined). Kaziba, 1140 m, 24 February 1948, 2 ♀ paratypes (Mission De Witte) (MRAC 139.413) (examined). Lusinga, 1810 m, 3 ♂ 2 ♀ paratypes (Mission De Witte) (MRAC 139.444) (examined).

Remark.—Holotype and paratypes of *straeleni* were discovered in the MRAC col-



Figures 1-3.—*Trabea straeleni*. 1, Male palp, ventral view; 2, Male palp, lateral view; 3, Epigynum. Scales: Figures 1-2 = 0.5 mm, Figures 3 = 0.1 mm.

lection. They are labelled as such most probably by Roewer. Apparently, Russell-Smith (1982) did not examine this type material. The lectotype he designated from material in SMF is here considered to be no longer valid.

Diagnosis.—Similar to *Trabea purcelli* Roewer but darker with a more conspicuous black fringe of hairs on male palp; terminal apophysis larger; lateral part of tegular apophysis more curved, and anterior edge of tegular apophysis with clear groove. Each set of spermathecae in a compact group.

Description.—*Male*: ($n = 2$) CW = 1.09 (1.11–1.07), CL = 2.80 (2.78–2.82), TL = 5.18 (5.24–5.12). Carapace dark brown with a pale median band and two continuous pale lateral bands. Sternum yellow. Chelicerae yellow with short, black stripes at its base. Clypeus mainly yellow. Abdomen with dorsal side pale brown and with two longitudinal, black stripes. Ventral side mainly yellow. Spinnerets yellow. Legs yellow. Femur I with two propapical spines and dorsally with two large spines beside a smaller apical one. Tibia I with

four pairs of ventral spines and an additional apical pair. Metatarsus I with three pairs of ventral spines and an additional apical pair. Palp: femur mainly yellow but darker ventrally. Patella proximal half yellow, distal half darker. Tibia and tarsus dark brown. Tibia with long black hairs laterally. Hairs almost as long as diameter of tibia.

Female: ($n = 2$) CW = 1.82 (1.68–1.96), CL = 2.80 (2.66–2.94), TL = 5.74 (5.60–5.88). Carapace paler than in male with broad pale median band and two continuous lateral bands. Sternum yellow. Chelicerae mainly yellow, with short black basal stripes. Clypeus yellow. Abdomen with dorsal side pale brown and with darker pattern of two longitudinal stripes. Ventrally mainly yellow. Spinnerets yellow. Legs light brown to yellow. Femora often with dark lateral stripes. Tibiae and metatarsi often with darker spots. Ventral spination of tibia and metatarsus I as in male. Palp yellow to light brown.

Other material examined.—**CONGO (ZAIRE)**: Lusinga, 1810 m, 16 July 1947, 1♂ (Mission De Witte) (MRAC 139.443). Upemba National Park, 1♂ (MRAC 139.896, sub *Pseudevippa bipunctata*). Upemba National Park, 2♂ (SMF, sub *Pseudevippa bipunctata*). **RUANDA**: Butare, campus de l'INRS, grassland, 6 November 1985, 1♂ (Jocqué, Nsengimana & Michiels) (MRAC 164.931). **MALAWI**: Vipha Mountains, Chikangawa, young pine plantation, September–October 1977, 4♂ (R. Jocqué) (MRAC 153.578). **ETHIOPIA**: 10 km E of Adis Ababa, grassland, *Pennisetum* tussocks, 2500 m, 8 June 1986, 2♂2♀ (A. Russell-Smith) (PCMA 815).

Distribution.—Congo (Zaire), Ruanda, Malawi and Ethiopia.

Trabea purcelli Roewer 1951

Figs. 4–6

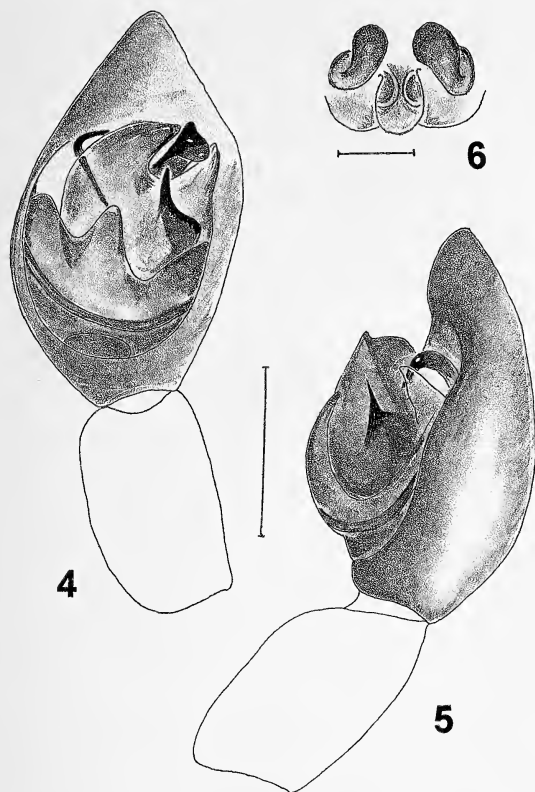
Trabaea lineata Purcell 1903: 130, fig. 20

Trabaea purcelli Roewer 1951: 442 (nom. nov.); Russell-Smith 1982: 74, fig. 11c

Trabaeosa purcelli: Roewer 1954: 297; Roewer 1960: 588, fig. 332.

Type material.—**SOUTH AFRICA**: Cape, Kogmanskloof, Ashton side, 27 August 1900, 1♀ holotype (W.F. Purcell) (SAM 6266) (examined).

Remarks.—Originally described by Purcell (1903) as *T. lineata* but due to preoccupation renamed *purcelli* by Roewer (1951). *Pseudevippa bipunctata* Roewer 1959 was earlier synonymized with *T. purcelli* (Alderweireldt



Figures 4–6.—*Trabea purcelli*. 4. Male palp, ventral view; 5, Male palp, lateral view; 6, Epigynum. Scales: Figures 4, 5 = 0.5 mm, Figure 6 = 0.1 mm.

1991). Due to the revalidation of *T. straeleni*, it became clear that *P. bipunctata* is in fact a junior synonym of the latter and not of *T. purcelli*.

Diagnosis.—Paler than *straeleni* with spermathecae further apart in a less compact group and median septum almost semi-circular. Terminal apophysis relatively smaller. Lateral part of tegular apophysis shorter. Anterior edge of tegular apophysis with poorly developed groove. Palpal cymbium and tibia less hairy.

Description.—*Male*: CW = 1.65, CL = 2.60, TL = 5.00. Carapace pale brown with a yellow median band and two continuous broad pale lateral bands. Sternum yellow with darker parts along sides. Chelicerae yellow, with darker longitudinal stripes. Clypeus mainly yellow. Abdomen faded, yellow in general, pattern probably not much different from other species. Spinnerets yellow. Legs yellow, the darker mottlings probably faded.

Tibia I with three pairs of ventral spines and an additional apical pair. Metatarsus I with three pairs of ventral spines and an additional apical pair. Palp yellow.

Female: (Coloration completely faded in alcohol; difficult to evaluate) ($n = 2$). CW = 1.95 (1.90–2.00), CL = 2.90 (2.80–3.00), TL = 5.40 (4.90–5.90). Carapace pale brown with yellow median band and two continuous lateral bands. Sternum yellow. Chelicerae yellow, with darker longitudinal stripes. Clypeus yellow. Abdomen faded, yellow in general, pattern probably not much different from other species. Spinnerets yellow. Legs yellow, no darker spots visible, probably faded. Ventral spination of tibia and metatarsus I as in male. Palp yellow.

Other material examined.—**SOUTH AFRICA**: Great Winterhoek Mountains, 4800–4900 feet, 17 November 1916, 1♂ (R.W. Tucker) (SAM 2776, sub *Trabea lineata*). Clanwilliam, November 1899, 1♀ (R.M. Lightfoot) (SAM 5880, sub *Trabea lineata*). Matroosberg mountains, 3500–4500 feet, 20 January 1917, 1♀ (R.W. Tucker) (SAM 2988, sub *Trabea lineata*). Waterfall mountains, November 1902, 1♀ (R.M. Lightfoot) (SAM 12388, sub *Trabea lineata*).

Distribution.—South Africa, Cape Province.

Trabea heteroculata Strand 1913

Figs. 7–9

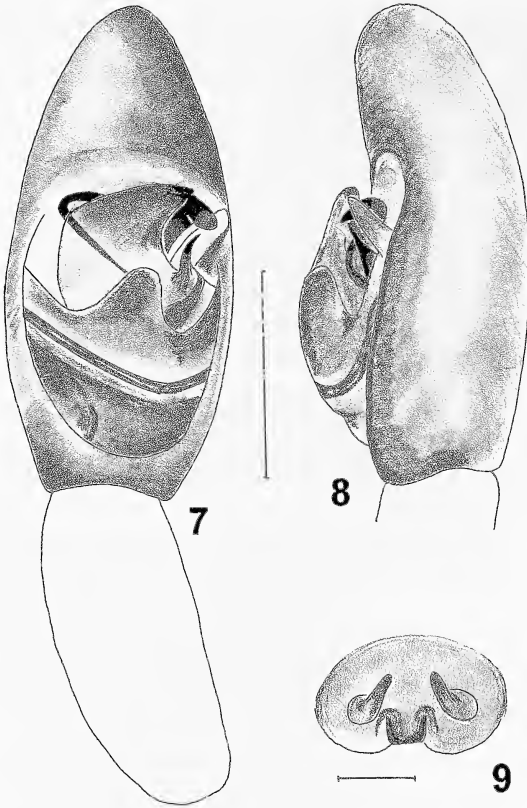
Trabea heteroculata Strand 1913: 456; Lessert 1926: 346, fig. 10; Caporiacco 1949: 338; Russell-Smith 1982: 84, fig. 8.

Trabeosa heteroculata Roewer 1954: 297; Roewer 1960: 583, fig. 330.

Type material.—**RUANDA**: Rugege forest, 1800 m, 20 August 1907, 1♀ holotype (Schubotz) (ZMB 10523) (examined).

Diagnosis.—Smaller and paler species than the others considered here. Vulva with spermathecae typically overlapping with one part oriented to ventral side. Cymbium of male rounded without lateral dent and with many flattened setae on tip. Palpal tibia short. Terminal apophysis relatively weak.

Description.—(Coloration somewhat faded in alcohol). *Male*: CW = 1.55, CL = 2.40, TL = 5.00. Carapace pale brown with broad pale median band and two continuous broad pale lateral bands. Sternum yellow with some faint darker spots near coxae. Chelicerae yellow with longitudinal, black stripes. Clypeus



Figures 7-9.—*Trabea heteroculata*. 7, Mirrored view of right male palp, ventral view; 8, Mirrored view of right male palp, lateral view; 9, Epigynum. Scales: Figures 7, 8 = 0.5 mm, Figure 9 = 0.1 mm.

yellow. Abdomen with dorsal side pale brown to yellow and with some black mottling forming two longitudinal stripes. Ventral side mainly yellow. Spinnerets yellow. Legs yellow, hardly any darker markings visible. Femur I with two pro-apical spines. Tibia I with three pairs of ventral spines and an additional apical pair. Metatarsus I with three pairs of ventral spines and an additional apical pair. Palp mainly yellow with some faint darker spots.

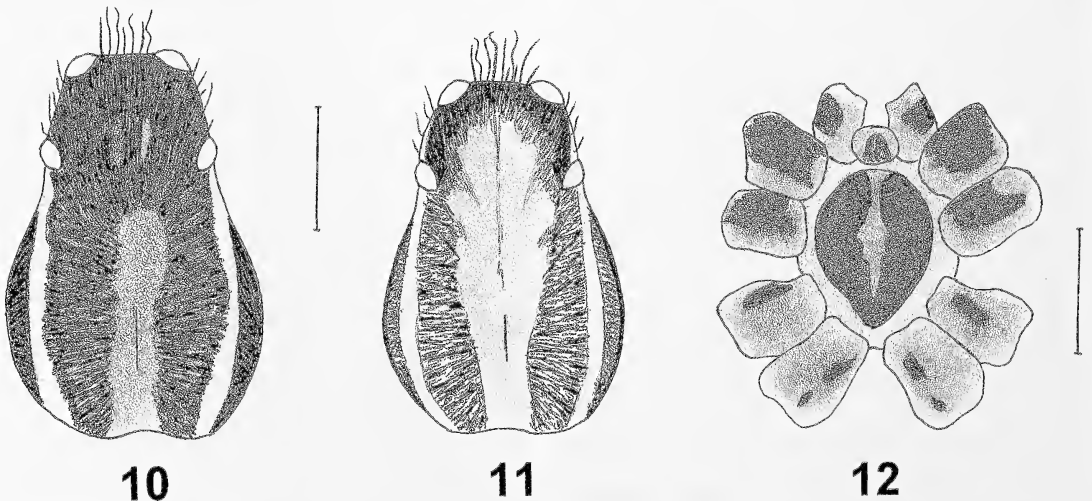
Female: ($n = 2$) CW = 1.75 (1.70–1.80), CL = 2.65 (2.60–2.70), TL = 4.85 (4.80–4.90). Carapace pale brown with broad pale median band and two continuous broad lateral bands. Sternum pale yellow. Chelicerae yellow, mostly with darker streaks. Clypeus yellow. Abdomen with dorsal side pale brown to yellow and with two longitudinal darker stripes, ventrally pale yellow. spinnerets yellow. Legs yellow with darker mottlings. Ventral spination of tibia and metatarsus I as in male. Palp yellow to light brown, without darker markings.

Other material examined.—TANZANIA: Kilimanjaro, Kiboscho, 3000 m, 1♂4♀ (Y. Sjöstedt) (NHRS). KENYA: Mount Kenya, July 1975, 1♀ (R. Bosmans) (MRAC 161.774).

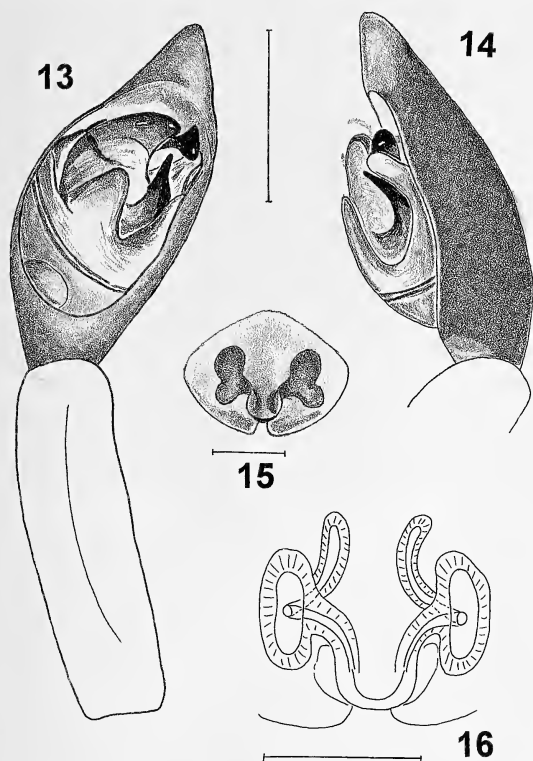
Distribution.—Ruanda, Tanzania and Kenya.

Trabea nigristernis new species
Figs. 10-16

Type material.—MALAWI: Mount Mu-



Figures 10-12.—*Trabea nigristernis* new species. 10, Male carapace, dorsal view; 11, Female carapace, dorsal view; 12, Male sternum. Scale = 1.0 mm.



Figures 13–16.—*Trabea nigristernis* new species. 13, Male palp, ventral view; 14, Male palp, lateral view; 15, Epigynum; 16, Vulva cleared. Scales: Figures 13, 14 = 0.5 mm, Figures 15, 16 = 0.1 mm.

lanje, Lichenya plateau, 2000 m, grassland in firebreak, 9–22 November 1981, 1♂ holotype (R. Jocqué) (MRAC 206.674). Chelinda, 2300 m, December 1981, 1♀ paratype (R. Jocqué) (MRAC 156.201).

Diagnosis.—Coloration similar to *Trabea heterocolata* but with dark sternum in male and without white hairs on cymbium. Palpal tibia long, somewhat curved and flattened on one side. Also resembling *Trabea ornatipalpis* Russell-Smith 1982 but shape of anterior edge of tegular apophysis, lateral part of tegular apophysis and terminal apophysis as well as vulva clearly different.

Description.—*Male:* ($n = 5$) CW = 1.99 (1.80–2.20), CL = 3.04 (2.70–3.30), TL = 5.66 (5.30–6.30). Carapace dark brown with pale median band and two continuous pale lateral bands. Lateral bands covered with white hairs becoming denser anteriorly. Sternum dark with pale median stripe not reaching posterior margin. Chelicerae yellow with longi-

tudinal, black stripes. Clypeus yellow with black markings. Dorsal side of abdomen brown with some black mottling and two longitudinal, black stripes; ventral side brown. Spinnerets blackish with yellow base. Legs yellow, some darker markings only on ventral and lateral side of femur I and II. Femur I with two pro-apical spines and dorsally with two large spines beside a smaller apical one. Tibia I with three pairs of ventral spines and an additional apical pair. Metatarsus I with two pairs of ventral spines and an additional apical pair. Palp femur yellow with darker base. Tibia yellow, patella and tarsus mainly black.

Female: ($n = 5$) CW = 2.04 (1.90–2.30), CL = 3.14 (3.00–3.50), TL = 6.12 (5.50–6.70). Carapace much paler than in male with broad pale median band and two continuous lateral bands covered with pale white hairs becoming denser in front. Sternum pale yellow with two darker stripes along sides. Chelicerae yellow, mostly with darker streaks. Clypeus yellow. Dorsal side of abdomen pale brown with two longitudinal stripes; ventrally pale with darker brown spots. Spinnerets yellow. Legs light brown to yellow. Femur I and patella I yellow with many darker brown markings. Tibia I and metatarsus I dark brown and tarsus I yellow. Ventral spination of tibia and metatarsus I as in male. Spines long and overlapping. Palp yellow to light brown, usually with darker spots and stripes.

Other material examined.—**MALAWI:** Mount Mulanje, Lichenya plateau, 2000 m, grassland and firebreak, 9–22 November 1981, 1♂1♀ (R. Jocqué) (MRAC 156.309). Mulanje path, 1850 m, 19 November 1981, 1♀ (R. Jocqué) (MRAC 156.657). Chilemba hill, 2300–2350 m, 20 November 1981, 1♂ (R. Jocqué) (MRAC 156.673). Chilemba hill, grassland and firebreak, 2000 m, 9–24 November 1981, 2♂ (R. Jocqué) (MRAC 155.833). Chilemba hill, CCAP hut, 2000 m, 5–25 November 1981, 1♀ (R. Jocqué) (MRAC 155.792). Linje pools, wet grassland, 2000 m, 5–22 November 1981, 1♂ (R. Jocqué) (MRAC 155.846). Linje river, Cliffortia vegetatie, 5–23 November 1981, 1♂ (R. Jocqué) (MRAC 155.750). Mount Mulanje, Chisepo shelter, 2120 m, 13 November 1981, 1♂1♀ (R. Jocqué) (MRAC 206.675). Nyika plateau, road to Kasaramba, 2350 m, grassland, 13 December 1981, 2♀ (R. Jocqué) (MRAC 156.691). Dambo, 2350 m, circular drive, 12 December 1981, 1♂1♀ (R. Jocqué) (MRAC 156.841). Chelinda, 2300 m, 7 December 1981, 2♀ (R. Jocqué) (MRAC 156.154). Chelinda, 2300 m, December 1981, 1♂ (R. Jocqué) (MRAC

156.217). Chelinda, 2300 m, by dam nr. 1, 3 December 1981, 1♂ (R. Jocqué) (MRAC 155.906). Lake Kaulime, 2200 m, 6–19 December 1981, 1♂ (R. Jocqué) (MRAC 156.018). Lake Kaulime, 2200 m, 6–19 December 1981, 1♂ (R. Jocqué) (MRAC 155.888). Dembo river, 2100 m, gradient from river to dry grassland, 5–20 December 1981, 1♂ (R. Jocqué) (MRAC 156.337).

Etymology.—The species name refers to the mainly dark sternum of the male which is unusual within the genus.

Distribution.—Malawi.

Trabea setula new species

Figs. 17–23

Type material.—MALAWI: Nyika plateau, Chelinda, 2300 m, burned grassland, 7–19 December 1981, 1♂ holotype (R. Jocqué) (MRAC 155.765). Chelinda, 2300 m, 7–19 December 1981, 5♂ paratypes (R. Jocqué) (MRAC 155.870).

Diagnosis.—Recognized by the row of small spines below posterior eyes on the lateral margin of cephalon.

Description.—*Male:* ($n = 5$) CW = 1.58 (1.50–1.65), CL = 2.28 (2.10–2.40), TL = 4.56 (4.30–4.90). Carapace dark brown with a broad pale parallel-sided median band and broad yellow lateral bands. Margin with fine black line. Some small black spines within pale yellow lateral bands. Row of 9–10 small, black spines below posterior eyes on lateral side of cephalon. Sternum yellow with small dark spots along coxae. Chelicerae yellow with brown stripes. Clypeus yellow. Abdomen with dorsal side brown and pale brown median band and two longitudinal rows of black spots. Ventrally brown. Spinnerets pale brown. Legs yellow with dark spots especially on ventral side of coxae and femora. Tibia I with three pairs of ventral spines and an additional apical pair. Metatarsus I with three pairs of ventral spines. Palp femur mainly yellow with dark inner and outer brown stripes. Inner brown stripe on femur with green to blue iridescence. Patella mainly dark but dorsally yellow. Tibia and tarsus black thickly covered with long black hairs. Tibia very short in comparison to many other *Trabea* species, including *nigristernis*.

Female: ($n = 2$) CW = 1.45 (1.40–1.50),

CL = 2.35 (2.30–2.40), TL = 5.20 (4.90–5.50). Carapace pale brown with very broad yellow median and lateral bands. Margin with fine black stripe. Many short black spines within yellow lateral bands. Subocular row of short spines clearly present on lateral side of cephalon. Spines, however, white in contrast to male. Sternum yellow with darker spots along coxae. Chelicerae yellow with brown stripes. Clypeus mainly yellow. Abdomen with dorsal side pale brown and broad yellow median band and darker spots. Ventral side mainly yellow. Spinnerets yellow. Legs yellow with dark spots. Tibia I ventrally with three pairs of spines and one apical pair. Metatarsus I with three pairs of ventral spines. Palp yellow.

Other material examined.—MALAWI: Nyika plateau, Chelinda, burned grassland, 7–10 December 1981, 1♂ (R. Jocqué) (MRAC 156.759). idem, 2300 m, 7–19 December 1981, 1♂ (R. Jocqué) (MRAC 155.943). idem, 2300 m, 7–19 December 1981, 2♂2♀ (R. Jocqué) (MRAC 155.738). idem, 2300 m, 7–19 December 1981, 1♂ (R. Jocqué) (MRAC 170.722). idem, 2300 m, 7–19 December 1981, 2♂ (R. Jocqué) (MRAC 206.676). idem, 2300 m, Cupressus plantation, 5 December 1981, 1♂ (R. Jocqué) (MRAC 156.228). idem, 2300 m, burned grassland in 1980, 7–19 December 1981, 1♀ (R. Jocqué) (MRAC 206.677).

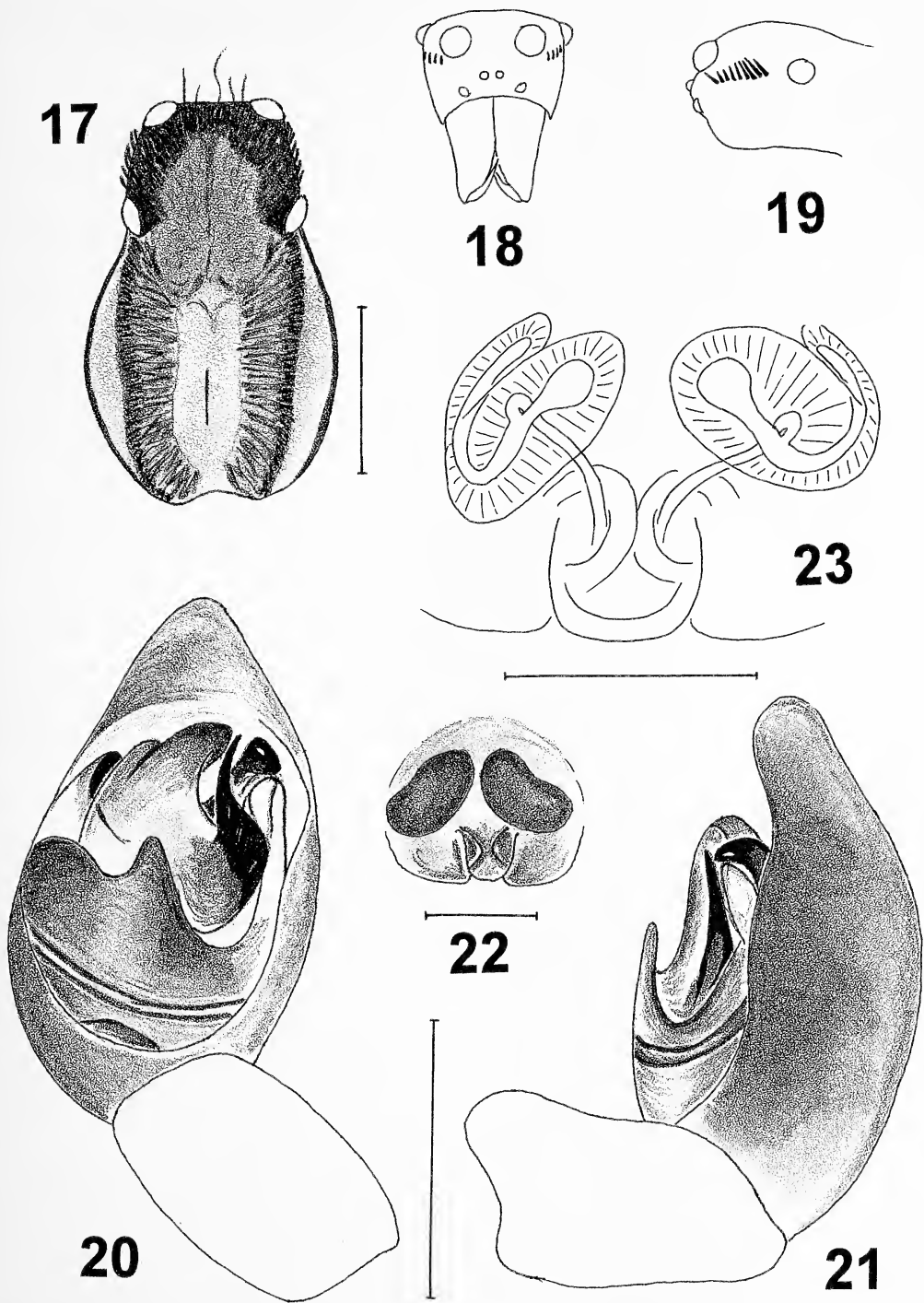
Etymology.—The species name refers to the row of small setae laterally on the cephalon below the posterior eyes.

Distribution.—Malawi.

Trabea ornatipalpis Russell-Smith 1982

Material examined.—SOUTH AFRICA: Cape Town, Table Mountain, summit, 30 March 1916, 1♀ (R.W. Tucker) (SAM 2474). Cape Town, Table Mountain, above Casteels poort, 27 February 1915, 1 subad. ♀ (R.M. Tucker) (SAM 910).

The epigynum of the female in SAM corresponds to that of *T. ornatipalpis* of which only females were known from Natal. These were matched with one male from Table Mountain in the Cape Province. The female from Table Mountain suggests that Russell-Smith (1982) was correct when matching males and females originally collected from very different localities.



Figures 17–23.—*Trabea setula* new species. 17, Male carapace, dorsal view; 18, Cephalon, frontal view, showing position of row of small spines; 19, Cephalon, lateral view, showing position of row of small spines; 20, Male palp, ventral view; 21, Male palp, lateral view; 22, Epigynum; 23, Vulva cleared. Scales: Figure 17 = 1.0 mm, Figures 20, 21 = 0.5 mm, Figures 22, 23 = 0.1 mm.

KEY TO CENTRAL AFRICAN *TRABEA* SPECIES, INCLUDING THE
SOUTHERN *PURCELLI*

1a.	Males	2
1b.	Females	6
2a.	Anterior edge of tegular apophysis without conspicuous groove (Figs. 7, 13); cymbium quite elongated (Figs. 7, 13) with group of modified hairs (flattened setae) on tip; palpal tibia without fringe of black hairs	3
2b.	Anterior edge of tegular apophysis with groove (Figs. 1, 4, 20) (most clearly visible in mesal view); cymbium shorter (Fig. 1) without group of modified hairs (flattened setae) on tip; palpal tibia usually with fringe of black hairs	4
3a.	Larger species; cymbium gradually narrowed in apical third (Fig. 13); palpal tibia as long as or longer than cymbium (Fig. 13), somewhat curved and flattened on one side; terminal apophysis strongly developed; sternum with large proportion dark (Fig. 12) . . . <i>nigristernis</i> new species	
3b.	Smaller species; cymbium blunt, hardly narrowed in apical third (Fig. 7); palpal tibia shorter than cymbium (Fig. 7); terminal apophysis smaller; sternum mainly yellow <i>heteroculata</i>	
4a.	Carapace on lateral side below posterior lateral eyes with short row of conspicuous black spines (Figs. 18, 19)	<i>setula</i> new species
4b.	Carapace without such a short row of spines	5
5a.	Lateral part of tegular apophysis strong and curved; anterior edge of tegular apophysis with deep groove (Figs. 1, 2); central Africa	<i>straeleni</i>
5b.	Lateral part of tegular apophysis relatively small and straight; groove of anterior edge of tegular apophysis inconspicuous, poorly developed (Figs. 4, 5); southern Africa	<i>purcelli</i>
6a.	Carapace on lateral side below posterior lateral eyes with short row of pale white but conspicuous spines (cf. Figs. 18, 19); spermathecae close to each other (Fig. 23); epigynal septum rounded (Fig. 22)	<i>setula</i> new species
6b.	Carapace without such a short row of spines; spermathecae usually further apart; epigynal septum rounded to square	7
7a.	Epigynal septum almost square, with conspicuous edges (Fig. 9); medial part of spermathecae directed ventrad (Fig. 9)	<i>heteroculata</i>
7b.	Epigynal septum rounded; medial spermathecae not directed ventrad	8
8a.	Epigynal septum with clear edges, not semi-circular; each set of spermathecae forming a compact group in the uncleared epigynum	9
8b.	Epigynal septum smoothly rounded, almost semi-circular (Fig. 6); each set of spermathecae further apart in a less compact group (Fig. 6)	<i>purcelli</i>
9a.	Epigynum as in Fig. 15; sternum with some darker parts along sides . . . <i>nigristernis</i> new species	
9b.	Epigynum as in Fig. 22; sternum normally completely yellow	<i>straeleni</i>

ZOOGEOGRAPHY

The genus *Trabea* seems to reach its highest diversity in South Africa with seven species occurring there. Besides this, two species are quite widespread in the Mediterranean area, north of the Sahara. Both these regions are amongst the better surveyed areas in Africa, and this might bias certain zoogeographical interpretations. In central and eastern Africa, four species are now known, two of which seem restricted to Malawi. Although extensive collections exist for instance from Congo (Zaire), only one *Trabea* species is known from that country.

The diversity observed in Malawi is striking but not new. In several other spider families and other arthropod groups, the mountain forest relicts seem to contain a special fauna. The new *T. setula* found in Malawi, Nyika

plateau is clearly closely related to *T. purcelli* known from the Cape. This again might be an indication of the historical connection between forested areas of both regions. However, there seems to be no reason why the genus should not be present in other geographically intermediate countries such as Zimbabwe, Botswana or Mozambique. As far as can be judged from the very poor biological data, most species are in no way restricted to forests (cf. Russell-Smith 1982). Both new species from Malawi are so far restricted to montane areas, as is the case for *T. ornatipalpis* from South Africa and *T. heteroculata* from Ruanda, Malawi and Tanzania.

CHECKLIST OF PALAEARCTIC AND
AFROTROPICAL *TRABEA* SPECIES

The following valid species of *Trabea* are now known from the African continent and

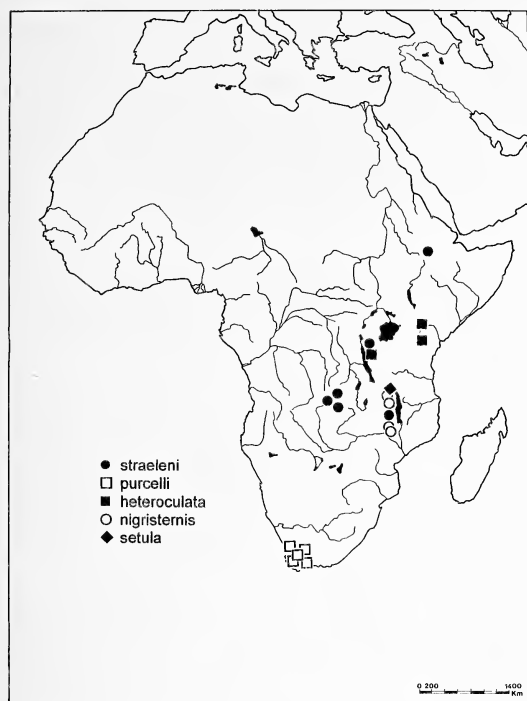


Figure 24.—Distribution of the *Trabea* species occurring in central Africa and of *T. purcelli* from South Africa.

the Mediterranean region: *cazorla* Snazell 1983 (Spain and north Africa, ♂ & ♀ known), *heteroculata* Strand 1913 (Ruanda, Tanzania and Kenya, ♂ & ♀ known), *natalensis* Russell-Smith 1982 (Natal, South Africa, only ♂ known), *nigriceps* Purcell 1903 (Cape, South Africa, ♂ & ♀ known), *nigristernis* new species (Malawi, ♂ & ♀ known), *ornatipalpis* Russell-Smith 1982 (Natal and Cape, South Africa, ♂ & ♀ known), *paradoxa* Simon 1876 (Mediterranean Europe and north Africa, ♂ & ♀ known), *purcelli* Roewer 1951 (Cape, South Africa, ♂ & ♀ known), *rubriceps* Lawrence 1952 (Natal and Cape, South Africa, only ♀ known), *setula* new species (Malawi, ♂ & ♀ known), *straeleni* Roewer 1960 (Congo (Zaire), Ruanda, Malawi and Ethiopia, ♂ & ♀ known), *unicolor* Purcell 1903 (Cape, South Africa, only ♂ known) and *varia* Purcell 1903 (Cape, South Africa, ♂ & ♀ known).

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**THE IDENTITY OF *PACHYLOIDES TUCUMANUS* N. COMB.
(EX *BOSQIA*), WITH A PROPOSAL OF GENERIC SYNONYMY
AND THE NEW NAME *PACHYLOIDES YUNGARUM*
(OPILIONES, GONYLEPTIDAE, PACHYLINAE)**

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ABSTRACT. The nominal genus *Bosqia* Canals 1933 is determined to be junior subjective synonym of *Pachyloides* Holmberg 1878. This results in the new combination *Pachyloides tucumanus* (Canals 1933) for the only species hitherto assigned to *Bosqia*, and in a secondary homonymy with *Pachyloides tucumanus* Canals 1943. For the latter, the new name *Pachyloides yungarum* is proposed. The article provides a redescription of *Pachyloides tucumanus* (Canals 1933) new combination, including the male external and genital morphology (previously unknown). New records of the species are also reported.

RESUMEN. Se determina la sinonimia del género nominal *Bosqia* Canals 1933 bajo *Pachyloides* Holmberg 1878. Este cambio resulta en la nueva combinación *Pachyloides tucumanus* (Canals 1933) para la única especie hasta ahora incluida en *Bosqia*, así como en la homonimia secundaria con *Pachyloides tucumanus* Canals 1943; para esta última especie se propone el nombre nuevo *Pachyloides yungarum*. El artículo presenta una redescrición de *Pachyloides tucumanus* (Canals 1933), comb. n., incluyendo la morfología externa y genital del macho, hasta ahora desconocido. Se proporcionan nuevos registros de la especie.

This paper deals with the identity of one of the poorest known gonyleptids of Argentina, which is the type and sole species of an equally neglected nominal genus. *Bosqia tucumana* was described by Canals (1933) on the basis of a single female, likely a subadult. For more than 60 years, this was the only material known to belong to the species. All further citations just refer to the original description.

In the scope of an ongoing systematic survey of the harvestmen of the Argentinian “yungas” (montane rainforests in the north-west of the country), I was able to gather some specimens which fit well in *Pachyloides* Holmberg 1878, but not to any species included in this genus. Those specimens seem to belong to a quite rare species, and appear at a first glance to be slightly more slender and long-legged than its congeners. As stated elsewhere, *Pachyloides* evidences a remarkable diversity in the yungas, especially on the eastern slopes of the Nevados del Aconquija and adjacent chains (province of Tucumán): to date, I have found in the whole area not less than 17 species and/or subspecies, among named and unnamed entities (Acosta 1996;

Acosta & Maury 1998). The genus now contains 15 nominate species, which, aside from the yungas elements, comprise the type species *Pachyloides thorellii* Holmberg 1878 and six south Brazilian species (in the future these six species may be excluded from the genus, see Acosta 1999).

Pachyloides was until recently defined by the tarsal formula 6:n [= “more than six”]: 7:7, but its diagnosis and scope were slightly modified, by adding to it species with 6 tarsomeres in legs III and IV (Acosta 1996). The character, number of tarsal segments has been—following the Roewerian thinking—somewhat misused before, and often just a difference of one tarsomere in one pair of legs was enough for the erection of a new generic entity (actually, except leg II, whose variability was deemed not to be relevant). It is now clear that such minimal difference, taken alone, is not only trivial but also useless at this level. Moreover, some *Pachyloides* species bear some degree of intraspecific variability in the involved pairs of legs (Acosta 1992, 1996).

All these considerations concern the defi-

dition of the nominal genus *Bosqia*. Seemingly, Canals (1933) decided to assign *tucumana* to a new genus (instead of relating it to an already named one) because of the "unique" tarsal formula 6:n:6:7. This feature and the supposedly unarmed ocular mound are the only two characters mentioned in the generic diagnosis that are different from *Pachyloides* (according to its traditional diagnosis, the latter has paired armature on the ocular mound). The study of the above mentioned "long-legged" *Pachyloides* revealed to me that this material and Canals' *Bosqia tucumana* are conspecific. The tarsal formula, alleged to be a generic character, is likely just an individual variant: only one specimen was known to Canals (right tarsus III actually lost!). Further, in some of the specimens I examined legs IV have 8 tarsomeres ($5/24 = 20.8\%$ of studied tarsi). Thus, even though the available material is still scarce, this species show unusual variation in this feature.

These observations lead to the following taxonomic and nomenclatural conclusions: (1) *Bosqia* is to be regarded as junior synonym of *Pachyloides*, confirming what I suspected in a previous paper (Acosta 1992); (2) This implies the new combination *Pachyloides tucumanus* for Canals' (1933) species; (3) Since there is another species *Pachyloides tucumanus* Canals 1943, a secondary homonymy arises: for the latter (junior homonym) I propose here the new name *Pachyloides yungarum*; (4) A further slight modification of the generic diagnosis of *Pachyloides* is needed: Tarsal formula will be now 6:n:6-7:6-8 (*cf.* diagnosis by Acosta 1996). The present article provides a redescription of *P. tucumanus* new combination (males are here described and illustrated for the first time), together with the formal proposal of the mentioned nomenclatural changes at generic and specific levels.

The following collections have been studied: BMNH = British Museum (Natural History); IML = Instituto Miguel Lillo, San Miguel de Tucumán; LEA = Collection of the author, Córdoba; MACN = Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires.

Pachyloides Holmberg

Pachyloides Holmberg 1878:72 [Type species: *Pachyloides thorellii* Holmberg 1878, by monotypy].

Pachyloides: Ringuelet 1959:351 [synonymy]. Acosta 1996:4 [= *Daguerreia*]

Daguerreia Canals 1933:5. Mello-Leitão 1939:619, 1935:98 [*"Daguerreia"*]. Soares & Soares 1954: 244 (in part). Ringuelet 1959:288 (in part). Acosta 1992:170 (in part).

Bosqia Canals 1933:8. Mello-Leitão 1935:98, 1939: 620. Soares & Soares 1954:238. Ringuelet 1959: 286. Acosta 1992:170. NEW SYNONYMY.

Pachyloides tucumanus (Canals) new combination

Figs. 1–7

Bosqia tucumana Canals 1933:8, fig. 3. Mello-Leitão 1939:620. Soares & Soares 1954:238. Ringuelet 1959:286. Galiano & Maury 1979:318.

NEC: *Pachyloides tucumanus* Canals 1943 (invalid by secondary homonymy; see new name below).

Type material.—Holotype female (MACN 4589): Anfama (Tucumán), June 1933, J.M. Bosq coll.; examined.

Type locality.—Anfama (1600 m), province of Tucumán, Argentina (26°45'S, 65°34'W).

Diagnosis.—Habitus more slender than congeners, with comparatively longer legs and pedipalps (*cf.* fig. 9); tarsal formula 6:n:6-7:6-8; ocular mound very low, with two small tubercles or unarmed; granulation on dorsal scutum inconspicuous; trochanter IV (male) with a lobulate prolateral apophysis, without a dorsoapical, finger-like apophysis; femur IV (male) with a retrolateral row of 8–10 apophyses. Excluding *Pachyloides maculatus* (Canals 1933), *P. tucumanus* new combination is the only *Pachyloides* in its range area lacking the mentioned finger-shaped apophysis on trochanter IV (*P. hades* Acosta 1989, *P. cochuna* Acosta 1996 and *P. yungarum* new name, all have this feature). *Pachyloides maculatus* is more robust and granulous, with very dark coloration; males bear a more complicated armature on the trochanter IV, though not the above cited apophysis (Canals 1933). There are two other species devoid of this apophysis, *P. sicarius* (Roewer 1925) and *P. borellii* (Roewer 1925), both having 6:n:6:6 tarsomeres and a higher ocular mound; additionally, the apophyses on males' femur IV are not equally-sized as in *P. tucumanus* new combination (Acosta 1992). *Pachyloides tucumanus* new combination shows the closest overall similarity to *P. sicarius*.

Distribution and habitat.—*Pachyloides tucumanus* new combination seems to be a

Table 1.—Measurements (mm) of female holotype and the illustrated male of *Pachyloides tucumanus* new combination.

	Holotype female	Male
Scutum length/maximal width	5.04/4.12	6.99/5.72
Prosoma length/width	1.95/2.60	2.48/3.09
Leg I, total/femur length	10.88/2.67	16.05/3.89
Leg II, total/femur length	16.30/3.98	26.25/6.31
Leg III, total/femur length	13.30/3.48	20.33/5.45
Leg IV, total length	17.70	27.70
trochanter	0.92	1.98
femur	4.34	6.44
patella	1.64	2.54
tibia	3.55	5.82
metatarsus	4.86	7.61
tarsus	2.39	3.31
Pedipalp, total/femur length	8.24/2.09	11.01/2.80
Chelicera, distal piece length/width	1.94/0.70	2.62/0.91
Ocular tubercle, width/height	0.83/0.23	1.01/0.34

rare species. The holotype and some material were collected in the “aliso” (*Alnus acuminata* H.B.K.) belt of the phytogeographic province of the Yungas (Brown 1995). Other specimens come from the subtropical rainforests belt (lower altitude) in the same phytogeographic unit. Known localities are restricted to the Argentinian province of Tucumán, on the eastern slopes of the Nevados del Aconquija chain; elevation of records ranges from about 800–1750 m. In its southernmost locality (La Banderita) I captured the species together with a form allied to *P. maculatus* (likely an unnamed subspecies) and a yet undescribed gonyleptid, belonging to the subfamily Metasarcinae Kury 1994 (Maury pers. comm.). Material from the Río Los Sosa valley was found with *Pachyloides maculatus* s.s., *Pachyloides yungarum* new name, and again the above cited Metasarcinae. *Pachyloides tucumanus* new combination share the type locality with *P. maculatus* (Canals 1933).

Description.—General coloration in most preserved specimens uniform pale hazel, only a single male dark hazel. Faint pigment covers the scutum, forming a reticulate pattern on the prosoma, on ventral and anterolateral part of coxa IV. Measurements of the holotype and illustrated male are given in Table 1. Dorsal scutum length: males from 6.9–7.3 mm (\bar{x} = 7.1 mm, n = 5), females from 5.0–6.3 mm (\bar{x} = 5.8 mm, n = 7). Prosoma almost without granules. Eye mound very low, bearing a pair of minute tubercles, sometimes lacking (e.g.,

the holotype). Scutum granulation in general less conspicuous, especially on the anterior areas, whilst granules become more pearl-like on area V and free tergites. Area I either undivided (6 of 12 individuals, among them the holotype), divided (4 of 12 individuals), or with longitudinal division incipient (2 of 12). Areas I–V and free tergites with one row of granules; and additional, sparse granulation on the anterior half of areas I–IV. Lateral areas with a row of granules. All appendages long and slender. Mesal-subapical spine of pedipalp femur strong. Legs I–III unarmed. Tarsal formula: 6:7–11:6–7:6–8 (6:7:6/lost:7 in the holotype). Variability of number of tarsomeres on legs II–IV is given in Table 2.

Male: Leg IV. Coxa smooth, with a strong, curved apophysis, slightly pointing sideways on dorsal view. Trochanter with a prolateral, lobulate apophysis on the anterior half; two small, acute apophyses on the posterior border: one dorsoapical, the other retroapical. Femur straight, with a slight dorsal thickening on its base; dorsal and prodorsal surfaces with rows of pearl-like granules; retrolateral row of about 8–10 acute apophyses, normally smaller proximally; proventral row of smaller apophyses, which ends in a larger, apical one; retroventral row—parallel to the former—of conic tubercles, ending in a retroapical apophysis (of equal size or larger than the proventral one); posterior border with two further, somewhat blunt apophyses (mediodorsal and retrodorsal). Patella and tibia covered by tiny,

Table 2.—Variation in number of tarsomeres on legs II, III and IV of *Pachyloides tucumanus* (Canals 1933) new combination.

Number of tarsomeres	6	7	8	9	10	11	n
Males							
Leg II	—	—	1	4	3	2	10
Leg III	—	10	—	—	—	—	10
Leg IV	1	5	4	—	—	—	10
Females							
Leg II	—	2	1	8	3	—	14
Leg III	1	12	—	—	—	—	13
Leg IV	—	13	1	—	—	—	14

acute granules, the latter segment bear three rows of taller ones: proventral, retroventral and retrolateral; in some specimens, the two former end in small apophyses (retroventral larger). Penis is illustrated in Figs. 4–6. *Female*: Scutum granulation much less conspicuous than male. Leg IV armed only with a short, acute apophysis on the prolateral side of coxa.

Discussion.—Since *Bosqia tucumana* was described from a female (this sex usually provides very few, if any, diagnostic characters in Pachylinae), I realize that assuming the holotype and the studied material to be conspecific may not be completely uncontroversial; nevertheless, several lines of evidence strongly support that view. Placed side by side, the females of that material and the holotype of *Bosqia tucumana* are indistinguishable with regard to, among other features, the eye mound (of about equal size as the median mound on the front border, cf. Figs. 7, 8), the relative length of legs, and the general granulation and shape of body. My survey in the yungas in the neighborhood of the type locality has so far detected two additional *Pachyloides* species: *P. maculatus* and *P. yungarum* new name. Females of the former are readily separated from *P. tucumanus* new combination by characters stated in the diagnosis (scutum coloration and granulation). For *P. yungarum* new name, its ocular mound is higher and armed with two conic apophyses or tubercles (cf. Figs. 7, 8); and, in addition, legs and pedipalps are comparatively shorter (Fig. 9).

The affinity of *P. tucumanus* new combination and *P. sicarius* may reveal a phylogenetic and biogeographic meaning. As I re-

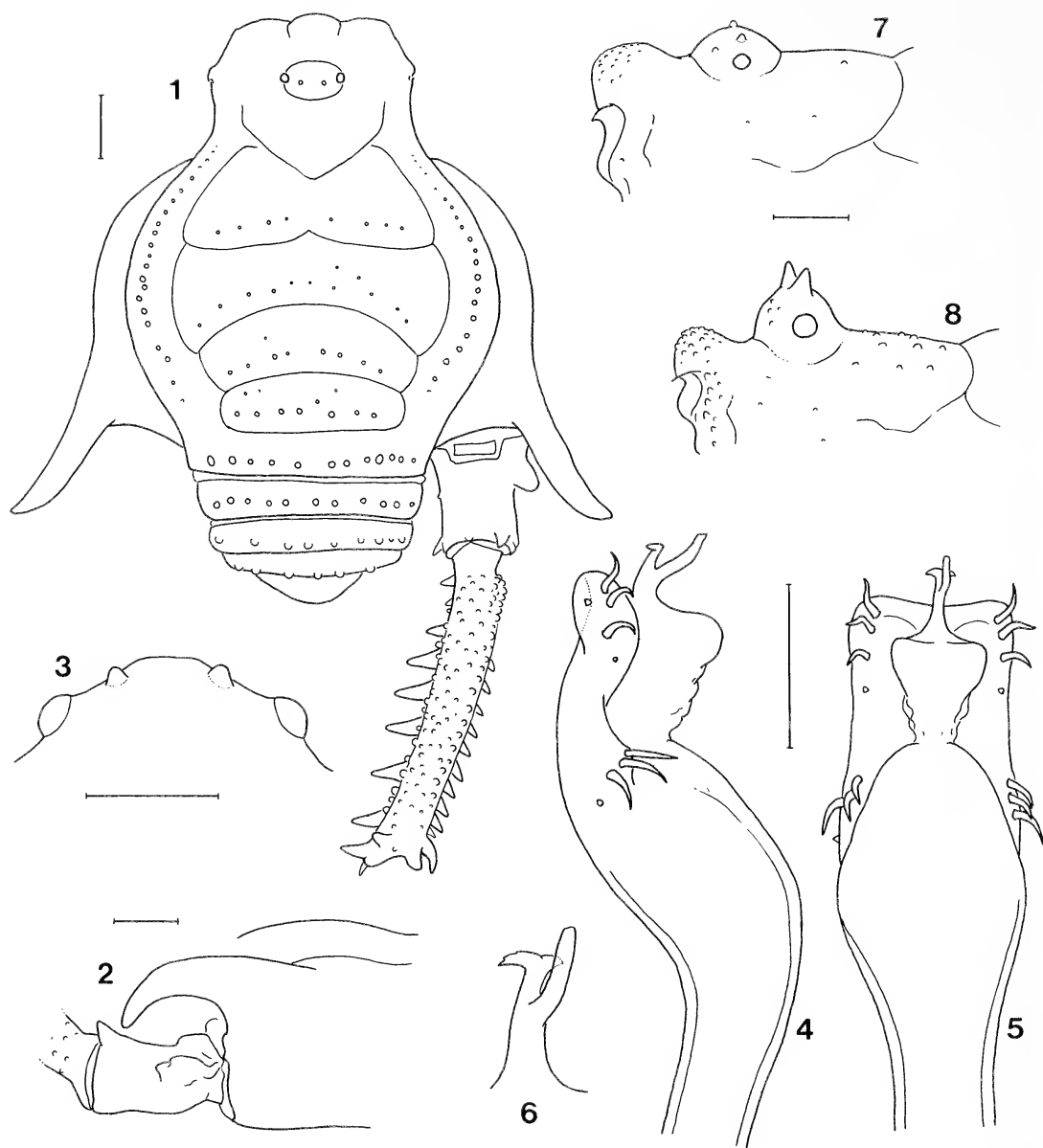
ported before (Acosta 1992, 1995), *P. sicarius* is known from the northern part of the Argentinian yungas and southern Bolivia, but an apparently isolated population was discovered 380 km south of the main range. Interestingly, localities of *P. tucumanus* new combination are placed between the two portions of *P. sicarius* range. The small dorsoapical apophysis on trochanter IV of male *P. tucumanus* new combination may have some kind of homology with a similar apophysis in *P. maculatus*, especially the unnamed subspecies, and even with that of *P. hades* (cf. Acosta 1989: figs. 1, 3). This structure is not present in *P. sicarius*.

New records.—**ARGENTINA:** *Province of Tucumán.* 2 km E from El Indio (845 m), 1 ♀, 11 February 1995 (L. Acosta, A. Peretti, M. Acosta, LEA); El Indio (940 m), 1 ♂, 17 January 1981 (A. Roig, MACN); Río Los Sosa (800–1000 m), 1 ♂ 1 ♀, November 1963 (W. Weyrauch, IML); La Banderita (1700–1750 m), 3 ♂ 4 ♀, 2 juv., 12 January 1993 (L. Acosta, D. Hauser, LEA).

Pachyloides yungarum new name

Pachyloides tucumanus Canals 1943:14, figs. 6, 7a, b. Soares & Soares 1954:283. Ringuelet 1957:19. Galiano & Maury 1979:321. Acosta 1989:137, figs. 9, 10, 1992:168, 170, 1996:2, 6, 9. NEC *Pachyloides tucumanus* (Canals 1933) new combination
Pachyloides thorelli tucumanus: Ringuelet 1959: 359.

Etymology.—The specific name *yungarum* (genitive plural) refers to the biogeographic unit called the “yungas,” whose southern one-third in Argentina (provinces of Salta, Tucumán and Catamarca) constitutes the habitat of this species.



Figures 1–8.—*Pachyloides tucumanus* (Canals 1933), new combination, and *Pachyloides yungarum* new name. 1–6, Male *Pachyloides tucumanus* from Río Los Sosa (IML). 1, Scutum, free tergites, coxae IV, right trochanter and femur IV, dorsal view; 2, Lateral view of right coxal apophysis IV and trochanter; 3, Eye mound, posterior view; 4–6, Penis glans. 4, Lateral view; 5, Dorsal view; 6, Detail of stylus; 7, Female *P. tucumanus* from 2 km E of El Indio (LEA), lateral view of eye mound and frontal border of prosoma; 8, Female *P. yungarum* from 10 km to El Siambón (LEA), lateral view of eye mound and frontal border of prosoma. Scale lines: Figs. 1, 2 = 1 mm; Figs. 3, 7, 8 = 0.5 mm; Figs. 4, 5 = 0.2 mm.

Type material.—Holotype male and allotype female (MACN 7151), 8 paratypes (MACN 7146), 1♂1♀ paratypes (BMNH 1955.2.22.76–77): Siambón (Tucumán), June 1933, J.M. Bosq coll., examined.

Type locality.—El Siambón (1000 m),

province of Tucumán, Argentina (26°45'S, 65°27'W).

Diagnosis.—Tarsal formula 6:n:6-7:6-7; ocular mound with a pair of conic apophyses; trochanter IV of male with a finger-shaped, dorsoapical apophysis, and a lobulate, prola-

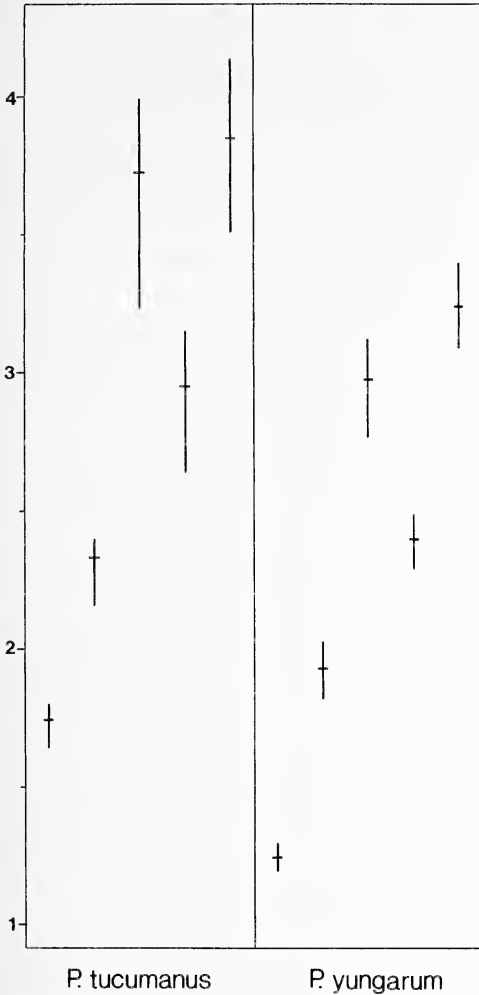


Figure 9.—Relative length of appendages [“total appendix length/scutum length” ratios] in female *Pachyloides tucumanus* (Canals 1933) new combination. ($n = 7$) and *Pachyloides yungarum* new name ($n = 5$; 10 km from El Siambón, province of Tucumán, Argentina; LEA). Vertical bars (range and mean) are from left to right: pedipalps and legs I–IV.

teral apophysis; femur IV of male with a regular row of small retrolateral apophyses. Nearest relative: *Pachyloides thorellii* Holmberg 1878 (Argentina: provinces of Buenos Aires, Córdoba, Entre Ríos; Uruguay); it can be separated from *P. yungarum* new name by the prolateral apophysis of trochanter IV (male), reduced in *thorellii* to a sclerotized ridge. Other similar species are *P. cochuna*, which has a distinctive tubercle under the normal apophysis on coxa IV (Acosta 1996), and *P. hades*,

with ocular tubercle lower and dorsoapical apophysis on trochanter IV more acute (Acosta 1989).

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NEW SYNONYMS IN THE GENERA *DISCOCYRTUS* AND *PACHYLOIDES* (OPILIONES, GONYLEPTIDAE, PACHYLINAE)

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ABSTRACT. To contribute to a depuration of the species-level taxonomy in the Gonyleptidae Pachylinae, the following synonymies are proposed: *Discocyrtus minutus* Roewer 1913 = *Discocyrtus testudineus* (Holmberg 1876); *Discocyrtus spinosus* Roewer 1916 and *Discocyrtus exceptionalis* Mello-Leitão 1933 = *Discocyrtus prospicius* (Holmberg 1876); *Pachylus spinosus* Canestrini 1888 (currently in *Pachyloides*) = *Discocyrtus dilatatus* Sørensen 1884; *Canalsia delicata* Mello-Leitão 1930 (removed from the synonymy of *Pachyloides iheringi* Roewer 1913) and *Pachyloides aelleni* Šilhavý 1979 = *Pachyloides thorellii* Holmberg 1878. All citations of *Discocyrtus affinis* Roewer 1913 from Argentina are referred to *D. prospicius* (the full synonymy is suspected but not formally proposed). References of *P. iheringi* from Argentina are determined to be *P. thorellii*. Comments on the type material, the type localities and on misidentifications of previous authors are included.

RESUMEN. A fin de contribuir a una depuración taxonómica en Gonyleptidae Pachylinae, se proponen las siguientes sinonimias: *Discocyrtus minutus* Roewer 1913 = *Discocyrtus testudineus* (Holmberg 1876); *Discocyrtus spinosus* Roewer 1916 y *Discocyrtus exceptionalis* Mello-Leitão 1933 = *Discocyrtus prospicius* (Holmberg 1876); *Pachylus spinosus* Canestrini 1888 (hasta ahora en *Pachyloides*) = *Discocyrtus dilatatus* Sørensen 1884; *Canalsia delicata* Mello-Leitão 1930 (excluida de la sinonimia de *Pachyloides iheringi* Roewer 1913) y *Pachyloides aelleni* Šilhavý 1979 = *Pachyloides thorellii* Holmberg 1878. Todas las referencias de *Discocyrtus affinis* Roewer 1913 para Argentina son referidas a *D. prospicius* (se sospecha la sinonimia plena de ambas especies, pero no se la propone formalmente). Se determina que las citas de *P. iheringi* para Argentina corresponden a *P. thorellii*. Se incluyen comentarios sobre el material típico, las localidades tipo y sobre los errores de identificación de autores previos.

One major hindrance in estimating the diversity of a given taxon is, no doubt, the persistence of nominal taxa with unclear status. The speciose subfamily Pachylinae (Gonyleptidae), which includes not less than 400 species, contains many entities described from a single or few specimens, chiefly by Roewer and Mello-Leitão. Because most of them were not further considered, or were merely mentioned in checklists, numerous doubtful situations and poorly known forms still persist. In recent years I have devoted my research to members of this subfamily from Argentina and neighboring countries. Through the study of several collections (types included) I was able to detect several species, hitherto assigned to the genera *Discocyrtus* Holmberg 1878 and *Pachyloides* Holmberg 1878, whose current status needs correction, either by invalidation through full synonymy, or deletion from the Argentinian checklist. The results given here contribute to the depuration of the

taxonomy of the group. The nomenclatural changes are indicated in abbreviated synonymies and briefly discussed below (references to where complete synonymies can be found are provided). Abbreviations of museums and collections are listed in the Acknowledgments section.

Discocyrtus testudineus (Holmberg)

Gonyleptes testudineus Holmberg 1876:29. *Type:* According to Holmberg (1876) it is "one example [male] in the Museum of the A.A. [= Academia Argentina], caught by [Rafael] Obligado and [Martin] Coronado (*loc. cit.*)" [Puerto Obligado, province of Buenos Aires, Argentina]; lost. *Discocyrtus testudineus*: Holmberg 1878:74. Ringuelet 1959:308 [complete synonymy for *D. testudineus*].

Discocyrtus minutus Roewer 1913:115, fig. 53. Roewer 1923:431, 437, fig. 548. Roewer 1929:202. Mello-Leitão 1932:167. Soares & Soares 1954:252. *Type:* Holotype male (SMF RI/796), "Argentinien: San Ignacio" (examined). NEW SYNONYMY.

Comments.—Although Ringuelet (1959), following Soares & Soares (1954), states that "one or more types" of *D. testudineus* would be in ZMC, in this collection there is no material with such label (only the specimens cited by Sørensen 1884 from "Riacho de Oro," "Villa Hernandaria" and "Baradero"). The holotype of *D. minutus* was mistakenly cited by Roewer (1913) from Bolivia, since the label states "Argentinien: San Ignacio" (Acosta 1996b), presumably in the Province of Misiones. In this specimen, apophyses of leg IV are less developed than usual, as it is commonly found in small males like this one.

Discocyrtus prospicius (Holmberg)

Gonyleptes prospicius Holmberg 1876:28. *Types*: "Several examples in our collection, captured in Las Conchas and near Palermo. There are some in the Museum of the University of Buenos Aires too" (Holmberg 1876); they are very likely lost. "Las Conchas" is today Tigre; Palermo is a quarter in the city of Buenos Aires.

Discocyrtus prospicius: Sørensen 1884:630. Ringuelet 1959:303 [complete synonymy for *D. prospicius*].

?*Discocyrtus affinis* Roewer 1913:117, fig. 54. *Types*: Syntypes, 2♂ (SMF RI/810, examined), "Brasilien" [in the original publication Roewer adds "São Paulo"; Acosta 1996b]. POSSIBLE SYNONYMY, see below.

Discocyrtus spinosus Roewer 1916:113, fig. 17. Roewer 1923:432, 438, fig. 551. Roewer 1929:203. Mello-Leitão 1932:168. Mello-Leitão 1939:624. Soares & Soares 1954:255. Ringuelet 1959:151, 196, 307. *Type*: Holotype ♂ (SMF RI/1315), "Argentinien: Bahía Blanca" (examined). NEW SYNONYMY.

Discocyrtus affinis: Roewer 1929:204, 205 (misidentification). Roewer 1938:6 (misidentification).

Discocyrtus exceptionalis Mello-Leitão 1933:59. Mello-Leitão 1939:623. Soares & Soares 1954:248. Ringuelet 1957:19, 23. Ringuelet 1959:196, 301. Capocasale 1966:635. *Type*: Holotype ♂ (MACN 4601), "Punta Rasa" [misspelling for Punta Lara, province of Buenos Aires, Argentina: Galiano & Maury 1979], August 1931, J. Daguerre coll. (examined). NEW SYNONYMY.

Comments.—Soares & Soares (1954) assumed that the types of *D. prospicius* are 8♂ and 6♀ deposited in ZMC. Very likely these are 14 specimens that Holmberg collected in Buenos Aires and gave to Sørensen, as cited by the latter (1884). Of them, only 5♂ and 3♀ remain. Since they were identified by Holm-

berg, these specimens may deserve special consideration, but there is no evidence that they are types.

The morphology of the femur IV characterizes males of *D. prospicius* (Acosta 1989), but the numerous femoral apophyses show variability. The dorsoproximal apophysis is most constant, while in retrodorsal position 1 or 2 apophyses may exist (rarely lacking). The retroventral apophysis is sometimes indistinguishable from the row of lower apophyses in that position. Though less developed (as usual in small specimens), apophyses of the holotype of *D. exceptionalis* show an identical pattern. The closeness of this species and *D. prospicius* was already mentioned by Ringuelet (1959), but considering two minor differences ("scutal area IV undivided" and "[bifid] apophysis of coxa IV with branches of the same length") he preferred to maintain its validity. I believe these supposed differences are insignificant; and they do not support any specific separation, hence the synonymy.

Also *D. affinis* might prove to be a junior synonym of *D. prospicius*. However, the types of the former show some slight differences in the apophyses pattern of femur IV of male; and for the moment it is difficult to determine whether they represent species, population or individual differences (more material from Brazil would be required). Nonetheless, citations of "*D. affinis*" from Argentina (Roewer 1929, 1938) are undoubtedly *D. prospicius*. *Discocyrtus affinis* is therefore excluded from the Argentinian checklist.

Material examined.—**ARGENTINA.** *Capital Federal*: "Buenos Aires" (Silv.), 1♂3♀ (MNHN, Coll. Simon 23383, det. *D. affinis* by Roewer 1925). *Province of Buenos Aires*: La Plata, 3♂1♀ (SMF RII 5841/100, det. *D. affinis* by Roewer 1935), 3♂1♀, Cpt. Kinberg coll. (NRS, det. *D. affinis* by Roewer 1935).

Discocyrtus dilatatus Sørensen

Discocyrtus dilatatus Sørensen 1884:627, 631. Acosta 1995:209 [complete synonymy for *D. dilatatus*].

Pachylus spinosus Canestrini 1888:108, pl. 9, fig. 1. *Type(s)*?: The author does not state how many specimens he studied, but at least a female from "Chaco australe" (likely the present Argentinian Province of Chaco) is illustrated. This material can no longer be found in Padova (A. Minelli *in litt.*) and is presumably lost. NEW SYNONYMY.

Pachyloides spinosus: Roewer 1913:98. Roewer 1923:431. Mello-Leitão 1939:621. Soares & Soares 1954:282. Ringuelet 1959:356 [*species inquirenda*]. Acosta 1996a:10 [ditto].

Comments.—Despite the brevity of the description, drawings of *Pachylus spinosus* show very clearly a female *Discocyrtus dilatatus* (cf. Canestrini 1888: fig. 1, and Acosta 1995: figs. 3–5); also the tarsal formula and approximate size agree. Indeed, it was Roewer (1913) who first assigned *spinosus* to *Pachyloides* (with doubts on the species identity, however), and the few subsequent authors just repeated the combination. Very probably Roewer (1913) took into account the supposedly unarmed scutum to place this species in *Pachyloides*; as I already stressed (Acosta 1995), the paired tubercles of area III are often difficult to distinguish from the dorsal granulation, especially in females. This feature led to some further confusion between these genera; e.g., Müller (1918) described two new Paraguayan species in *Pachyloides* (*fischeri* and *tuberculatus*), but both were synonymized under *D. dilatatus*, too (Acosta 1995).

Pachyloides thorellii Holmberg

Pachyloides Thorellii Holmberg 1878:72. *Types*: Two males (syntypes), from Buenos Aires (“Estación Central del Ferrocarril del Norte”), Feb. 1876, E.L. Holmberg coll., and San Martín, province of Buenos Aires, E. Aguirre coll. (both specimens lost).

Canalsia delicata Mello-Leitão 1930:137, 140, fig. 1. Mello-Leitão 1939:620. Soares & Soares 1954: 241. *Type*: Holotype female (MACN 4696), Buenos Aires, Feb. 1910, A. Frers coll. (examined). Formerly synonymized under *Pachyloides iheringi* Roewer 1913 (Ringuelet 1956). NEW SYNONYMY.

Parabalta borellii: Mello-Leitão 1931:81 [male from San Antonio de Areco, misidentified].

Pachyloides iheringi: Ringuelet 1956:19 [= *Canalsia delicata*, synonymy incorrect]. Ringuelet 1959:353 [misidentification]. Galiano & Maury 1979:318.

Pachyloides thorelli thorelli: Ringuelet 1959:356 (in part) [complete synonymy for *P. thorellii*, but discard citations listed below under “Nec”].

Parabalta sicaria: Ringuelet 1959:365 [the same male of Mello-Leitão 1931, misidentified]. Ringuelet 1962:2 [male from Alta Gracia, misidentified].

Pachyloides aelleni Šilhavý 1979:322, figs. 1–5. *Types*: According to Šilhavý, holotype male and paratype male, in the same vial (MHNG); only the former is now found in the collection, together

with two minute vials, each containing one male genitalia (examined): Gruta de Arequita, Lavalleja, Uruguay, 15 February 1968 (P. Strinati). NEW SYNONYMY.

NEC: Sørensen 1895:2. Roewer 1925:16. Roewer 1929:201. Ringuelet 1959:358 (part.) [citations from province of Tucumán].

Comments.—In *P. thorellii*, morphology of males and females may not differ so sharply as usual in Pachylinae. The prolateral apophysis of coxa IV of females is larger than in other *Pachyloides* species, though still shorter than in most males. In addition, females of this species are unique in the genus in bearing a small dorsal apophysis on the trochanter IV, which represents the well developed, finger-shaped apophysis of the male (Canals 1943:16). Sex identification is complicated by the presence of “feminoid” males (4/30 in the studied material). This overlap makes it necessary to observe genitalia in all “female-shaped” specimens to determine sex with certainty (“normal” males are easily recognizable). Ringuelet (1959) was obviously unaware of this fact, and in many cases he determined the sex of his material incorrectly. Ringuelet also overlooked the variability of the number of tarsomeres on legs III–IV; because of this, he erroneously identified as “*Parabalta sicaria*” Roewer 1925 any *Pachyloides* specimen bearing 6 tarsomeres in those legs. As I stated before (Acosta 1992 1996a), Ringuelet’s citations of “*Parabalta sicaria*” are all misidentifications, and they include three different *Pachyloides* species (*P. thorellii*, *P. yungarum* Acosta 1999, *P. cochuna* Acosta 1996a), but not the true *sicaria*. Ringuelet’s misuse of the character, number of tarsomeres is emphasized by a simple fact: *P. sicarius* is easily distinguishable from the above cited three *Pachyloides* species by the lack (in *sicarius*) of a finger-like apophysis on trochanter IV of male. In the material of *P. thorellii* I studied, 11% of the tarsi III and 6% of the tarsi IV bear 6 tarsomeres instead of 7. This is more frequent in females, and asymmetry is also common.

Ringuelet (1956) puts *Canalsia delicata* in the synonymy of *Pachyloides iheringi* Roewer 1913, but the holotype of the former is a female *P. thorellii*. All materials cited as “*P. iheringi*” by Ringuelet (1959) are indeed *P. thorellii*, including the alleged “allotype male” (designation by Ringuelet 1959, not

valid), which is actually a female. Consequently, also *P. iheringi* is now excluded from the Argentinian fauna. Syntypes of *P. iheringi* are two females (examined), one deposited in ZMB (2492), the remaining presumably in SMF (RI/799) (Acosta 1996b); it is clear that they do not correspond to Ringuelet's concept. Roewer (1913) mentions the type locality doubtfully ["Argentinien oder Uruguay? (genaue Loc.?)"], but labels state "Santa Cruz" (Acosta 1996b), presumably Santa Cruz do Sul (State of Rio Grande do Sul, Brazil). *Pachyloides iheringi* is very similar to other Brazilian "*Pachyloides*": *P. bellicosus* Roewer 1913, *P. calcartibialis* Roewer 1916, *P. armatus* Roewer 1916, *P. fallax* 1932 and *P. taurus* Mello-Leitão 1937. These six species very likely form a monophyletic group, and do not show any special similarity with *Pachyloides s.s.*; and they may actually represent a different genus (Acosta, 1996a).

Another species to be synonymized to *P. thorellii* is *P. aelleni*, captured in an Uruguayan cave (Gruta de Arequita). The type of the latter coincides exactly to the external and genital male morphology of *P. thorelli*. This synonymy, together with a couple of males collected in a cave in Province of Buenos Aires, constitutes further records of *P. thorellii* from caves (Capocasale 1968 cited the species from "Gruta Salamanca," Uruguay). As already reported, this species is known to be quite ubiquitous. Ringuelet (1959) considers it to be synantropic, since it is commonly found in houses and gardens in the cities of Buenos Aires and La Plata. I studied material found in such unusual places as in subterranean vaults of the telephone network in Buenos Aires. Maury (pers. comm.) even caught a specimen in the bathroom of the Museo Argentino de Ciencias Naturales! Captures in ant nests are also known (Acosta 1989). Confirmed records of this species come from the Argentinian provinces of Buenos Aires, Entre Ríos and Córdoba, and from southern Uruguay. Citations from Tucumán (cf. Sørensen 1895:2; Ringuelet 1959:358) correspond without doubt to *Pachyloides yungarum* Acosta (1999), as are also Roewer's references (1925, 1929) from "Cala" (El Tala), province of Salta (SMF RII: 264/9, examined. Materials he cited from Museo di Zoologia di Torino are no longer mentioned in Catalogues).

New records.—**ARGENTINA:** *Capital Federal*. Subterranean telephone vaults, Constitución St.-Saenz Peña St. corner, 1♂1♀, 19 June 1963 (A. Ibarra Grasso) (MACN), Santiago del Estero St. -Humberto 1° St. corner, 1♂1♀, 15 October 1969 (E. Maury) (MACN); "Buenos Aires", 2♀, November 1937 (J.B. Daguerre) (MACN 4698, det. as "2 males" *Pachyloides iheringi* by Ringuelet, one designated as "allotype"); same loc. (E.V. Gemignani) 1♀ (MACN 4700, formerly 10958, det. *Pachyloides iheringi* by Ringuelet, "young male" illustrated in fig. 50). *Province of Buenos Aires*. San Antonio de Areco, 1♂, 23 November 1920 (A.G. Frers) (MACN 4743, det. *Parabalta borellii* by Mello-Leitão, *Parabalta sicaria* by Ringuelet); Baradero, 2♂, 18 January 1916 (A.G. Frers) (MACN 4699, det. *Pachyloides iheringi* by Ringuelet); Cueva Matilde Catriel, Sierras Bayas, 2♂, December 1996 (P. Quaglia) (MACN). *Province of Entre Ríos*. Chajarí, 2♂1♀, 30 June 1977 (M. Viana) (MACN). *Province of Córdoba*. Alta Gracia, 1♂, 1 juv., February 1934 (C. Bruch) (MACN, det. *Parabalta sicaria* by Ringuelet).

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THERMAL TOLERANCES AND PREFERENCES OF THE CRAB SPIDERS *MISUMENOPS ASPERATUS* AND *MISUMENOIDES FORMOSIPES* (ARANEAE, THOMISIDAE)

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ABSTRACT. *Misumenops asperatus* (Hentz 1847) and *Misumenoides formosipes* (Walckenaer 1837) are diurnally-active, flower-dwelling crab spiders (Thomisidae) commonly inhabiting open fields. In laboratory experiments, both species remained active over a temperature range of approximately 46 °C. The spring-maturing *M. asperatus* tolerated significantly lower temperatures than the summer-maturing *M. formosipes* ($CT_{min} = -1.4$ °C and 2.2 °C, respectively), while *M. formosipes* tolerated significantly higher temperatures than *M. asperatus* ($CT_{max} = 48.2$ °C and 45.1 °C, respectively). *Misumenops asperatus* displayed thermal discomfort over a broader range of temperatures (36–44 °C) than did *M. formosipes* (41–46 °C). In a laboratory thermal gradient apparatus *M. asperatus* tended to prefer cooler temperatures than *M. formosipes* (14.4 °C and 18.4 °C, respectively). Regression analysis of literature data for 21 species of spiders showed a significant positive relationship between the thermal preference of a species and its CT_{max} . For their CT_{max} 's, which were high compared to most other spider species, *M. asperatus* and *M. formosipes* preferred low temperatures. The coupling of low thermal preferences and high thermal tolerances displayed by *M. asperatus* and *M. formosipes* is unusual for ectothermic organisms.

Spiders are strict ectotherms (Humphreys 1987; Pulz 1987) and are important predators in many terrestrial systems (Riechert 1974; Wise 1993), yet the thermal ecology of spiders is generally less well understood than is that of their insect prey (Humphreys 1987). Thermal relations (i.e., thermoregulatory behaviors, thermal tolerances and preferences) have been examined in less than 0.1% of spider species (Humphreys 1987), and most research has concentrated on large tropical and subtropical orb-weavers (e.g., Krakauer 1972; Carrel 1978; Robinson & Robinson 1978), desert-dwelling spiders (e.g., Mouer & Eriksen 1972; Seymour & Vinegar 1973; Humphreys 1974, 1987; Riechert & Tracy 1975; Lubin & Henschel 1990; Henschel et al. 1992; Turner et al. 1993), and winter-active species (e.g., Aitchison 1978). Studies of temperate-zone spiders inhabiting moderate environments have generally focused on cold resistance and super-cooling capabilities (e.g., Almquist 1970; Kirchner 1973, 1987; Schaefer 1977; Duman 1979; Bayram & Luff 1993) or temperature effects on growth and metabolic rate (e.g., Anderson 1970; Hagstrum 1970; Moulder & Reichle 1972; Li & Jackson 1996). Fewer studies have examined thermal prefer-

ences, upper tolerance limits, or thermoregulatory behaviors of spiders inhabiting temperate regions (for exceptions see Almquist 1970; Sevacherian & Lowrie 1972; Tolbert 1979; Suter 1981; references from Table 2 in Pulz 1987).

Information regarding an animal's thermal tolerances and preferences is necessary to describe the thermal ecology of the animal and to evaluate the thermal suitability of its habitat (Hertz et al. 1993). In the experiments reported here, I examined the thermal tolerances and preferences of two flower-dwelling crab spiders (Thomisidae), *Misumenops asperatus* and *Misumenoides formosipes*. These experiments were part of a larger study investigating temperature effects on crab spider microhabitat selection and hunting performance. Because *M. asperatus* and *M. formosipes* prey primarily on insect pollinators, most foraging opportunities and predation events occur diurnally (Schmalhofer 1996). Compared to nocturnal spiders, which are active when heat stress is minimal, *M. asperatus* and *M. formosipes*, as well as other diurnally-active inflorescence spiders, likely experience greater temperature variability and extremes of temperature. Consequently, diurnal spiders might

tolerate greater thermal stress. This study specifically addressed the following questions: 1) What are the thermal tolerances and preferences of *M. asperatus* and *M. formosipes*? 2) When comparing field-active adult female spiders, does the summer-maturing species, *M. formosipes*, display higher tolerances and preferences than the spring-maturing species, *M. asperatus*? 3) How do the thermal tolerances and preferences of these flower-dwelling thomisids compare with the thermal tolerances and preferences of other spiders? 4) Does data drawn from the literature indicate that diurnally-active spiders, in general, have higher thermal tolerances and preferences than nocturnally-active spiders?

Information concerning the thermal relations of *M. asperatus* and *M. formosipes* is of additional interest because thomisids rank among the most diverse families of spiders (Coddington & Levy 1991) and are among the most common cursorial spiders found in the herb stratum of open fields. However, the thermal ecology of this family is virtually unknown, consisting only of a few anecdotal observations (Morse 1979; Lockley et al. 1989).

METHODS

Study animals.—*Misumenops asperatus* and *M. formosipes* are sit-and-wait ambush predators that use their raptorial forelimbs, rather than a web, to restrain prey. In central New Jersey, *M. asperatus* matures in spring (mid-April to early May), females lay a single egg sac in late May or June, and spiderlings emerge in June and July and overwinter as late instar juveniles (pers. obs.). *Misumenoides formosipes* matures in mid-summer (August), females lay a single egg sac in September or early October, and spiderlings generally overwinter in the egg sac (pers. obs.).

Only adult female spiders were used in these experiments. Like many other spiders, male *M. asperatus* and *M. formosipes* seldom capture prey as adults, instead spending their time searching for and guarding prospective mates (Foelix 1996; Dodson & Beck 1993; Pollard et al. 1995). Spiders were collected in Middlesex and Somerset Counties, New Jersey, and voucher specimens have been deposited at the American Museum of Natural History. Experiments involving *M. asperatus* occurred in May and June 1993, and experiments involving *M. formosipes* occurred in

August 1993. A given spider was used in only one experimental manipulation.

Because hunger has been shown to influence thermal sensitivity in spiders (Pulz 1987), I maintained the experimental spiders on a diet of one housefly per week for three weeks prior to the initiation of the experiments. This regimen equalized hunger-states among individuals of a given species and maintained spider body mass at relatively constant levels (Anderson 1970; Schmalhofer unpubl. data).

Misumenops asperatus and *M. formosipes* were not acclimated to similar temperatures in the lab prior to testing. Although this confounds species identity with seasonal temperature differences when comparing the two species, I was not attempting to separate these influences, but, rather, was interested in comparing the responses of field-active adults. Also, other researchers (e.g., Sevacherian & Lowrie 1972; Seymour & Vinegar 1973) have found that temperature acclimation does not affect thermal preferences or upper tolerance limits of spiders. However, I maintained spiders at ambient field temperature, rather than a constant temperature, to reduce any possibility of spider responses to experimentally induced temperature changes being influenced by acclimation to an artificial temperature regime. Under natural conditions, the two species experienced different temperature regimes; average daily temperature, based on data collected from the weather station at the Hutcheson Memorial Forest Research Center (HMF) in Somerset County, New Jersey (the site of later field experiments), for 30 days prior to the initiation of experiments was 16.5 ± 8.7 °C for *M. asperatus* and 22.8 ± 7.9 °C for *M. formosipes*.

Thermal tolerances.—Critical thermal maximum (CT_{max}) and critical thermal minimum (CT_{min}) describe the highest and lowest temperatures, respectively, at which an animal is capable of displaying coordinated locomotory behavior (i.e., the animal can still escape unfavorable temperatures). An animal's thermal tolerance range is delimited by these critical temperatures. Outside its tolerance range an ectotherm enters a state of heat stupor or cold torpor, which may result in death if exposure to extreme temperatures is prolonged. Critical temperatures of *M. asperatus* and *M. formosipes* were determined by placing spi-

ders confined in petri dishes in a controlled temperature box (VWR Scientific model 2015 low-temperature incubator) initially set to 25 °C. Box temperature was then raised to 50 °C (to determine CT_{max}) or lowered to -5 °C (to determine CT_{min}). Temperature changed at a rate of approximately 1 °C every five minutes. This rate of change was similar to that used in other studies examining tolerance limits (e.g., Almquist 1970; Krakauer 1972; Seymour & Vinegar 1973). For every temperature change of 1 °C, the spiders were prodded to ascertain their ability to initiate an escape response. The last temperature at which a spider responded to prodding (by moving away from the probe, raising its raptorial forelimbs, or grabbing hold of the probe) was recorded as its critical temperature. Spiders were removed from the temperature box once they ceased to respond to prodding. Spiders are known to spontaneously initiate vigorous activity at high temperatures preceding CT_{max} ; this activity indicates thermal discomfort as maximal tolerance is approached (Lubin & Henschel 1990). The temperature ranges over which *M. asperatus* and *M. formosipes* displayed thermal discomfort were noted. Five spiders of each species were used to determine CT_{max} , and five different spiders of each species were used to determine CT_{min} (total $n = 10$ spiders per species). Another set of spiders ($n = 9$) was prodded at five minute intervals under constant temperature conditions (25 °C) to ascertain whether a lack of response to prodding was due to habituation rather than temperature.

Thermal preferences.—A temperature arena was established by placing a box (50 cm \times 50 cm), the bottom of which was demarcated into numbered squares (2 cm \times 2 cm), in a controlled temperature room at 2 °C. By-tac Teflon[®] paper lined the sides of the box to prevent spiders from escaping. A 650 W photoflood lamp (equivalent color temperature 3400 K) mounted on a ringstand and suspended 1 m above a corner of the arena served as a radiant heat source. A temperature map of the arena was created by determining the temperature of each square within the arena; a spider model (freeze-dried female thomisid) with a fine thermocouple attached to the ventral side of its abdomen was placed in each square and, after two minutes, its temperature

was recorded with a Bailey BAT-12 thermocouple thermometer.

Spiders were released singly into the center of the arena, and the number of each square in which a spider stopped and the amount of time it stayed within the square was recorded during a 10 minute period. A spider's preferred temperature (T_p) was determined according to the formula

$$T_p = \Sigma[(T_i)(t_i/t_q)]$$

where T_i is the temperature (°C) of square i , t_i is the time (s) spent in square i , and t_q is the total time (s) a spider was quiescent ($n = 9$ spiders per species). The preferred temperature range of a species was calculated as one standard deviation around its average T_p .

Field temperature.—Temperature data obtained from the weather station at HMF were averaged over three years (1993–1995) to determine average monthly high and low temperatures. These data were compared with the preferred temperature ranges of *M. asperatus* and *M. formosipes*. By graphing the data and calculating the appropriate area encompassed within the high-low temperature curves, a rough estimate of the frequency with which mature female spiders experienced ambient temperatures (shaded air temperature) within their preferred ranges was determined. Average daily temperatures calculated over a ten day period at the beginning and end of a species' adult stage were compared to determine the seasonal temperature shifts experienced by adult *M. asperatus* and *M. formosipes*.

Analyses.—Due to small sample sizes, nonparametric statistics were used to analyze the results. A Mann-Whitney U test was used to compare CT_{min} data of *M. asperatus* and *M. formosipes*. Because CT_{max} and thermal preference data of *M. asperatus* and *M. formosipes* were also compared to CT_{max} and thermal preference data of other spider species taken from the literature, Kruskal-Wallis tests were used, and all possible pairwise posthoc comparisons were made using Mann-Whitney U tests, with a Bonferroni correction for multiple comparisons (adjusted $\alpha = 0.009$). Spider species for which data were available in the literature were separated into two groups: diurnally active and nocturnally active. For comparative purposes, species that were active both nocturnally and diurnally were counted as diurnally active. Information con-

Table 1.—Critical thermal tolerances (CT_{max} 's and CT_{min} 's) and preferred temperatures (T_p 's) of *Misumenops asperatus* and *Misumenoides formosipes*, and the range of temperature over which spiders displayed thermal discomfort. Values are in °C. Critical thermal values and preferred temperatures are given as means (± 1 SD). For CT_{min} data, a significant difference occurs at $\alpha = 0.05$; for CT_{max} and T_p data, adjusted $\alpha = 0.009$.

Measurement	<i>M. asperatus</i>	<i>M. formosipes</i>	Mann-Whitney <i>U</i> test	<i>P</i> -value
CT_{min}	-1.4 (0.6)	2.2 (1.8)	-2.660	0.0098
CT_{max}	45.1 (1.3)	48.2 (0.2)	-2.627	0.0086
T_p	14.4 (3.4)	18.4 (5.4)	-1.810	0.0703
thermal discomfort	36-44	41-46		

cerning the activity times of the various species came from the original studies and from Roberts (1995). In cases where information concerning a species' activity time could not be found, the species was presumed to be nocturnally active. Literature values for CT_{max} and T_p were subjected to simple linear regression to determine whether CT_{max} increased with increasing T_p .

RESULTS

Thermal tolerances.—Cessation of spider responses to prodding was due to temperature, not habituation to prodding. Under constant temperature conditions, spiders did not become habituated in 45 consecutive prodding trials. In the CT_{min} and CT_{max} experiments, a given spider was prodded less than 30 times. Also, spider posture changed noticeably when critical temperature was reached. Throughout most of the experimental temperature range, spiders maintained the classic crab spider hunting posture (raptorial forelimbs held outstretched, slightly upraised, and approximately perpendicular to the long axis of the body). Within approximately 1 °C of upper or lower critical temperature, spiders abandoned the classic hunting posture and huddled with their forelimbs held close to the body.

Misumenops asperatus and *M. formosipes* proved to be broadly temperature tolerant. *Misumenops asperatus* had a significantly lower CT_{min} than did *M. formosipes* (Table 1). Conversely, *M. formosipes* had a significantly higher CT_{max} than did *M. asperatus* (Table 1). Spontaneous initiation of escape behavior by spiders (i.e., a spider moved vigorously around the petri dish without prompting from the investigator) was observed during the CT_{max} experiments, and *M. asperatus* dis-

played thermal discomfort over a wider temperature range than did *M. formosipes* (Table 1). No evidence of low-temperature thermal discomfort was observed during the CT_{min} experiments (i.e., there was no period of spontaneous activity).

Values for the CT_{max} 's of other spider species are presented in Table 2. Comparing CT_{max} values of *M. asperatus* and *M. formosipes* with literature data for diurnally-active and nocturnally-active spiders revealed significant differences (Kruskal-Wallis test: $H = 16.271$, $df = 3$, $P = 0.001$). Diurnal spiders and nocturnal spiders had similar CT_{max} 's, and diurnal spiders and *M. asperatus* had similar CT_{max} 's (Fig. 1). However, CT_{max} 's of *M. asperatus* and nocturnal spiders differed significantly, and *M. formosipes* had a significantly higher CT_{max} than *M. asperatus*, nocturnal spiders, or diurnal spiders (Fig. 1).

Thermal preferences.—Temperature in the experimental arena ranged from 9–57 °C. Spiders encountering hotter areas moved rapidly to cooler areas, holding their bodies well-elevated above the substrate (stilting) until they settled in a cooler section of the arena. Although spiders moved more slowly (relative to the speed at which they vacated hot areas) at the cooler end of the arena, no evidence of cold-trapping (i.e., spider activity was so reduced by the cold that they could not emigrate from cooler areas) was observed. Spiders did not stilt in areas cooler than 30 °C. *Misumenops asperatus* preferred cooler temperatures than *M. formosipes*, but this trend was not significant (Table 1).

Preferred temperatures of other spider species are presented in Table 2. Comparing T_p 's of *M. asperatus* and *M. formosipes* with lit-

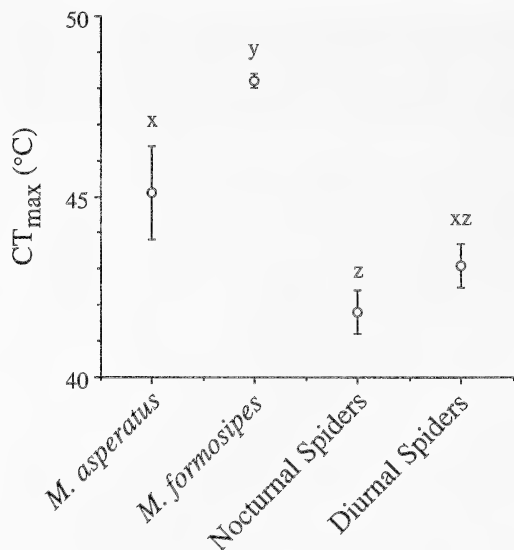


Figure 1.—Critical thermal maxima (CT_{max}'s) of *Misumenops asperatus*, *Misumenoides formosipes*, nocturnally-active spiders and diurnally-active spiders. Data for nocturnal and diurnal spiders were taken from Table 2; winter-active species were not included in the analysis. Values with different letters are significantly different using post-hoc Mann-Whitney *U* tests with adjusted $\alpha = 0.009$. Error bars represent one SE for nocturnal and diurnal spiders and one SD for *M. asperatus* and *M. formosipes*. Standard errors could not be used for *M. asperatus* and *M. formosipes* since species averages were calculated from individual values. In contrast, nocturnal and diurnal averages were calculated from species averages, making use of the standard error appropriate.

erature data for diurnally-active and nocturnally-active spiders revealed significant differences (Kruskal-Wallis test: $H = 23.878$, $df = 3$, $P \leq 0.0001$). Preferred temperatures were similar between *M. formosipes* and *M. asperatus*, and between *M. formosipes* and nocturnal spiders (Fig. 2). However, T_p 's of *M. asperatus* and nocturnal spiders differed significantly, and T_p of diurnal spiders was significantly higher than that of *M. formosipes*, *M. asperatus*, or nocturnal spiders (Fig. 2).

Relationship between CT_{max} and thermal preference.— Using the literature data shown in Table 2, a significant positive relationship was found between a spider species' T_p and its CT_{max} ($F = 6.707$, $df = 1$, 19 , $P = 0.018$, $r^2 = 26.1\%$) (Fig. 3). Because *M. asperatus* and *M. formosipes* had unusually high CT_{max}'s for their T_p 's, data for these two species were

not included in this analysis. Addition of *M. asperatus* and *M. formosipes* data to the regression resulted in a loss of the significant relationship ($F = 1.615$, $df = 1$, 21 , $P = 0.2177$, $r^2 = 7.1\%$). For similar reasons, data for winter-active spiders were also excluded.

Field temperature.—*Misumenoides formosipes* experienced preferred temperatures under field conditions more frequently than did *M. asperatus*. Ambient temperature fell within the preferred temperature range (PTR) of adult *M. asperatus* 43% of the time, exceeded PTR 47% of the time, and fell below PTR 10% of the time (Fig. 4). In contrast, ambient temperature fell within PTR of adult *M. formosipes* 65% of the time, exceeded PTR 10% of the time, and fell below PTR 25% of the time (Fig. 4). During their adult phase, *M. asperatus* experienced an increase in average daily temperature of 5.3 °C, and *M. formosipes* experienced a decrease in average daily temperature of 6.5 °C.

DISCUSSION

Comparing the thermal tolerances and preferences of the spring-maturing *M. asperatus* with those of the summer-maturing *M. formosipes* yielded the expected results. Adult female *M. asperatus*, which experienced lower ambient temperatures than did adult female *M. formosipes*, had a lower CT_{min}, while *M. formosipes* had a higher CT_{max}. Thermal preferences of the two crab spider species were similar. Of greater interest is a comparison of the thermal tolerances and preferences of these flower-dwelling spiders with those of other spider species.

There is little information available regarding CT_{min} in spiders. In the single study of which I am aware, Hagstrum (1970) reported a CT_{min} of 6 °C for a southern California wolf spider, *Alopecosa kochi* (Keyserling 1877) (as *Tarentula kochi* in Hagstrum 1970). Much more data is available concerning lower lethal temperatures and temperature effects on developmental rates (e.g., Almquist 1970; Li & Jackson 1996). Data from other studies indicates that temperate-climate spiders are generally capable of activity at relatively low temperatures. Ford (1978) showed that a European wolf spider, *Pardosa amentata* Clerck 1757, remained active at 5 °C, and Moulder & Reichle (1972) obtained similar results for the litter-spider fauna of a Tennessee *Lirio-*

dendron forest. Aitchison (1984) found that both winter-active and winter-inactive Canadian spiders fed at 2 °C, with winter-active species continuing to feed at temperatures as low as -5 °C. These studies, coupled with the CT_{min} values calculated for *M. asperatus* and *M. formosipes*, suggest that temperate-zone spiders from moderate climates may generally be expected to have CT_{min} 's near 0 °C.

Misumenops asperatus, and particularly *M. formosipes*, had high thermal tolerances. In general, CT_{max} 's of these flower-dwelling thomisids were more similar to the upper lethal temperatures than to the CT_{max} 's of other spider species (see Table 2). Of the 27 species for which data was available, only six species had comparable CT_{max} 's: *Phurrolithus festivus* (C.L. Koch 1835), *Euophrys frontalis* (Walckenaer 1802), *Cyrtophora citricola* (Forskål 1775), *Zelotes longipes* (L. Koch 1866) (as *Z. serotinus* in Almquist 1970), *Hogna carolinensis* (Walckenaer 1805) (as *Lycosa carolinensis* in Moeur & Eriksen 1972), and *Seothyra henscheli* (Dippenaar 1991). *Misumenoides formosipes* had the second highest CT_{max} recorded for a spider; only *S. henscheli*, an eresid from the Namib desert (Lubin & Henschel 1990), had a higher thermal tolerance. The natural histories of *M. asperatus* and *M. formosipes* may provide an explanation for their unusually high thermal tolerances. These thomisids do not stalk prey, but, rather, position themselves close to a flower's nectaries and/or anthers (pollen-bearing structures) in order to ambush flower-visiting insects (pers. obs.). On the plants used by *M. asperatus* and *M. formosipes*, the floral surface from which nectaries and anthers are accessed by insects is typically exposed to the sun (pers. obs.). Under conditions of high radiant intensity and low wind speed, body temperatures of spiders on sun-exposed floral surfaces can exceed ambient temperature by 15 °C or more (Schmalhofer 1996). A high thermal tolerance would allow *M. asperatus* and *M. formosipes* to continue hunting at ambient temperatures near 30 °C, when floral surface temperatures could be in excess of 40 °C. Ambient temperatures approaching 30 °C are not an uncommon occurrence in late spring and summer in central New Jersey: from April through September in 1993–1995 there were, on average, 52 days per year having a daily high temperature of at least 30 °C.

One would expect that because diurnally-active spiders experience higher temperatures than nocturnally-active species, diurnally-active spiders would prefer higher temperatures. Evaluation of data from the literature showed that this was indeed the case (Fig. 2). However, T_p 's of *M. asperatus* and *M. formosipes* were lower than those of other diurnally-active species, and T_p of *M. asperatus* was also lower than that of nocturnally-active species! Pulz (1987) suggested that, barring winter-active spiders, lower thermal preference correlates with lower thermal tolerance. Regression analysis of the available literature data supported Pulz's hypothesis of a positive relationship between T_p and CT_{max} . Interestingly, the CT_{max} 's of *M. asperatus* and *M. formosipes* predicted from the regression equation (40.2 °C and 41.3 °C, respectively) were much lower than the measured values; alternatively, predicted T_p 's (32.1 °C and 43.4 °C, respectively) were much higher than the measured values. Thus, depending on how one looks at it, *M. asperatus* and *M. formosipes* have exceptionally high thermal tolerances or exceptionally low thermal preferences. This combination of high thermal tolerance and low thermal preference is unusual for an ectotherm; preferred temperature is usually nearer the upper than the lower tolerance limit (May 1985).

Broad temperature tolerances and relatively low thermal preferences displayed by *M. asperatus* and *M. formosipes* may be viewed as adaptations that facilitate their diurnal predatory lifestyles in potentially thermally stressful habitats (sun-exposed flowers). Hymenopterans and dipterans comprise most of the prey captured by these thomisids (Schmalhofer 1996). Dipterans are well known for their ability to fly at low temperatures (reviewed in Heinrich 1993); and large hymenopterans, such as honeybees and bumblebees, require thoracic temperatures of 30–35 °C in order to fly (reviewed in Heinrich 1993). The capacity to endothermically generate heat by shivering wing muscles allows these bees to fly at low ambient temperatures; honeybees can fly when ambient temperature is as low as 15 °C, and some bumblebees can fly when ambient temperature is less than 10 °C (reviewed in Heinrich 1993). Both *M. asperatus* and *M. formosipes* prey on honeybees, and *M. formosipes* is also capable of capturing bumble-

Table 2.—Literature values for critical thermal maxima (CT_{max} s), preferred temperatures (T_p s), and upper (T_{UL}) and lower (T_{LL}) lethal temperatures of various spider species. Values are presented in °C. "Code" describes the period of activity and climatic zone inhabited by a species: n—nocturnal hunter, n*—presumed nocturnal hunter (information unavailable), d—diurnal hunter, n/d—hunts nocturnally and diurnally, 1—temperate-zone species inhabiting a moderate environment, 2—presumed to be a temperate-zone species inhabiting a moderate environment, 3—winter-active temperate-zone species, 4—desert species, 5—tropical or subtropical species. Other symbols within the table are as follows: †—average value based on multiple values or the endpoints of a range of values given in the source, HS—heat stupor (this measure is higher than CT_{max} and indicates that locomotor capacity has been lost).

Spider	code	CT_{max}	T_p	T_{UL}	T_{LL}	Source
Agelenidae						
<i>Agelena consociata</i> Denis 1965	d, 5		23.0			table 2 in Pulz 1987
<i>Agelena labyrinthica</i> Clerck 1757	d, 2	41.5†HS	23.5†	45.0		table 2 in Pulz 1987
Araneidae						
<i>Argiope trifasciata</i> Forskål 1775	d, 1			53.7†		table 2 in Pulz 1987
<i>Cyrtophora citricola</i> Forskål 1775	n/d, 5	46.0HS	27.0†			table 2 in Pulz 1987
Clubionidae						
<i>Clubiona diversa</i> O. P.-Cambridge 1862	n, 1	41.4	22.3			Almqvist 1970
<i>Clubiona similis</i> L. Koch 1866	n, 1	42.1†	22.3		-9.5†	Almqvist 1970
<i>Clubiona trivialis</i> C. L. Koch 1843	n, 1	42.1	16.0		-8.3	Almqvist 1970
Dictynidae						
<i>Nigma walckenaeri</i> Roewer 1951 (as <i>Dictyna viridissima</i> in Pulz 1987)	n*, 4			48.2†		table 2 in Pulz 1987
Eresidae						
<i>Seothyra henscheli</i> Dippenaar 1991	n/d, 4	49.0				Lubin & Henschel 1990
Gnaphosidae						
<i>Zelotes longipes</i> L. Koch 1866 (as <i>Z. serotinus</i> in Almqvist 1970)	n, 1	46.4	23.1			Almqvist 1970
Linyphiidae						
<i>Bolyphantes index</i> Thorell 1856	n*, 3	39.6HS	4.1			table 2 in Pulz 1987
<i>Frontinella communis</i> Hentz 1850	d, 1	41.8		44.0		Suter 1981
<i>Macrargus rufus</i> Wider 1834	n*, 3	40.8†HS	1.2†			table 2 in Pulz 1987
<i>Oedothorax apicatus</i> Blackwall 1850	n*, 1	40.6†	17.1		-6.8	Almqvist 1970
<i>Stemonyphantes lineatus</i> L. 1758	n, 1	40.5	14.4		-11.1	Almqvist 1970
Liocranidae						
<i>Agroeca proxima</i> O. P.-Cambridge 1871	n, 1	37.4	19.4			Almqvist 1970
<i>Phurilithus festivus</i> C. L. Koch 1835	d, 1	45.6	27.5			Almqvist 1970
<i>Scotina gracilipes</i> Blackwall 1859	n, 1	41.4	16.8		-7.1	Almqvist 1970

Table 2.—Continued.

Spider	code	CT _{max}	T _p	T _{UL}	T _{LL}	Source
Lycosidae						
<i>Arctosa alpigena</i> Doleschall 1852	n/d, 2			47.3		table 2 in Pulz 1987
<i>Hogna carolinensis</i> Walckenaer 1805 (as <i>Lycosa carolinensis</i> in Moeur & Eriksen 1972)	n/d, 4	47.0		48.0		Moeur & Eriksen 1972
<i>Pardosa</i> spp.	n/d, 2			45.0†		table 2 in Pulz 1987
<i>Pardosa lugubris</i> Walckenaer 1802 (as <i>P. chelata</i> in Pulz 1987)	n/d, 2		26.2†	47.7		table 2 in Pulz 1987
<i>Pardosa nigriceps</i> Thorell 1856	n/d, 1	39.7	21.0			Almqvist 1970
<i>Pardosa pullata</i> Clerck 1757	n/d, 1		23.7†	45.1		table 2 in Pulz 1987
<i>Pardosa pullata</i>	n/d, 1		32.0†	43.0		table 2 in Pulz 1987
<i>Pardosa ramulosa</i> McCook 1893	n/d, 2		28.1†			Sevacherian & Lowrie 1972
<i>Pardosa sierra</i> Banks 1898	n/d, 2		34.6†			Sevacherian & Lowrie 1972
<i>Pirata piraticus</i> Clerck 1757	n/d, 1		29.0†	35.3		table 2 in Pulz 1987
<i>Pirata piraticus</i>	n/d, 1		21.0†			table 2 in Pulz 1987
<i>Trochosa robusta</i> Simon 1876	n/d, 2	40.4 ^{HS}	24.8			table 2 in Pulz 1987
<i>Trochosa spinipalpis</i> F. O. P.-Cambridge 1895	n/d, 2	39.3	19.2			table 2 in Pulz 1987
Philodromidae						
<i>Philodromus aureolus</i> Clerck 1757	n/d, 1	41.8†	23.1		-10.8	Almqvist 1970
<i>Tibellus oblongus</i> Walckenaer 1802	n/d, 1	42.8	19.0		-9.3	Almqvist 1970
Salticidae						
<i>Eucphrys frontalis</i> Walckenaer 1802	d, 1	45.7	27.5			Almqvist 1970
Tetragnathidae						
<i>Nephila clavipes</i> L. 1767	d, 5	41.6				Krakauer 1972
Theraphosidae						
<i>Aphonopelma</i> sp.	n, 4	43.0	29.0†			Seymour & Vinegar 1973
Theridiidae						
<i>Achaeranea riparia</i> Blackwall 1834 (as <i>Theridion saxatile</i> in Pulz 1987)	n*, 2			48.0†		table 2 in Pulz 1987
<i>Crustulina guttata</i> Wider 1834	n*, 1	41.8	19.6			Almqvist 1970
<i>Dipoena inornata</i> O. P.-Cambridge 1861	n*, 1	43.2	15.5			Almqvist 1970
Zoridae						
<i>Zora spinimana</i> Sundevall 1833	d, 1	41.8	19.5			Almqvist 1970

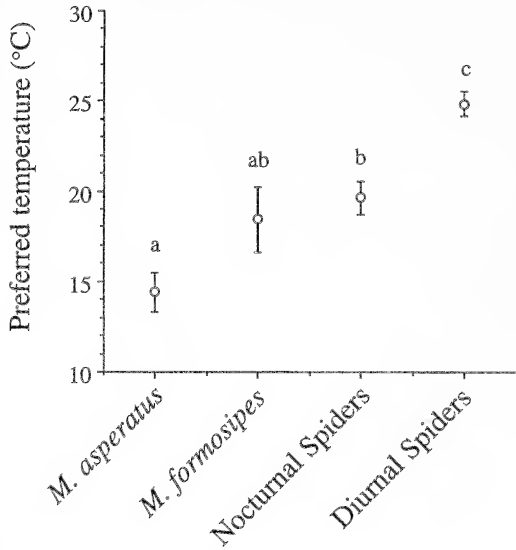


Figure 2.—Preferred temperatures of *Misumenops asperatus*, *Misumenoides formosipes*, nocturnally-active spiders and diurnally-active spiders. Data for nocturnal and diurnal spiders were taken from Table 2; winter-active species were not included in the analysis. Values with different letters are significantly different using post-hoc Mann-Whitney *U* tests with adjusted $\alpha = 0.009$. Error bars represent one SE.

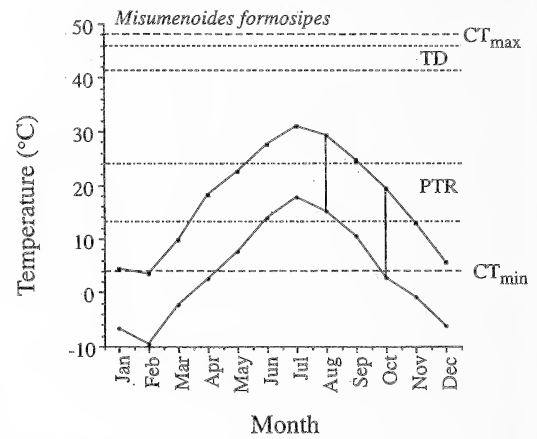
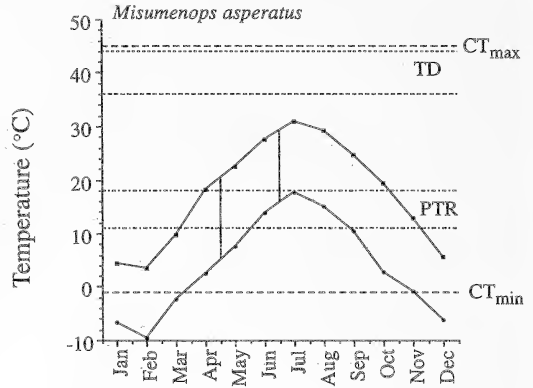


Figure 4.—The relationship between average daily high and low temperatures and the preferred temperature ranges (PTR's) of *Misumenops asperatus* and *Misumenoides formosipes*. Periods of adult activity are demarcated with vertical bars. CT_{max} (upper dashed line), CT_{min} (lower dashed line), and zone of thermal discomfort (TD, dotted lines) are indicated for each spider species. The bounds of a species' PTR (dot-dashed lines) were calculated as one standard deviation around mean T_p .

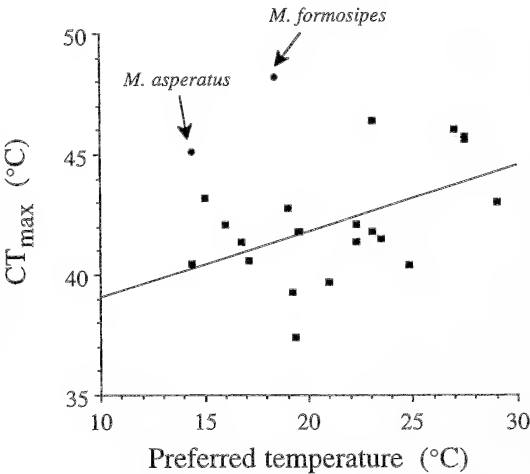


Figure 3.—Linear regression of preferred temperature against CT_{max} . The regression was based on literature data presented in Table 2. Regression equation: $y = 0.275x + 36.26$. Although not included in the regression, for comparative purposes data points for *Misumenops asperatus* and *Misumenoides formosipes* were included in the graph. Squares (■) represent other spiders species, circles (●) represent *M. asperatus* and *M. formosipes*.

bees (Schmalhofer 1996). Presumably many of the other bees used by these spiders, such as anthophorids and megachilids, display temperature-flight relationships similar to those shown by honeybees and bumblebees. The broad temperature tolerances shown by *M. asperatus* and *M. formosipes* allow these spiders to increase their foraging time, both daily and seasonally. Coupled with their ability to hunt equally well over a wide range of temperatures (Schmalhofer 1996), and their low thermal preferences, broad thermal tolerances benefit these spiders by affording them the op-

portunity to hunt prey that is itself active over a wide range of environmental temperatures.

Assuming that an ectotherm benefits by maintaining body temperature within some preferred range of temperature (Hertz et al. 1993), comparing preferred temperature ranges (PTR's) of *M. asperatus* and *M. formosipes* with the average range of temperatures normally experienced by these spiders allows one to make predictions concerning the likelihood that the spiders will experience thermal stress (i.e., unfavorable temperatures that might limit activity or impair performance). Data indicate that *M. asperatus* experiences high thermal stress (ambient temperature > PTR) more frequently than low thermal stress (ambient temperature < PTR), while *M. formosipes* experiences low thermal stress more frequently than high thermal stress. In neither case did average daily low temperature fall below spider CT_{min} . Thus, since ambient temperature did not fall to levels that would inhibit spider movement, *M. asperatus* and *M. formosipes* could alleviate low thermal stress by engaging in behaviors designed to elevate body temperature (e.g., basking in the sun). Normal hunting behavior (i.e., sitting near a flower's nectaries and/or anthers, provided the position was exposed to the sun) would serve to achieve this result.

High thermal stress appears to be more of a concern for these thomisids since ambient temperature typically falls within or above a spider's preferred range, and even when ambient temperature falls within the preferred range, floral-surface temperatures, and thus spider body temperatures, may be much higher, potentially approaching CT_{max} . Most diurnally-active spiders avoid high, stressful temperatures by some behavioral mechanism (Pulz 1987). Ground- or vegetation-dwelling cursorial (non-web-building) spiders can move to shaded areas under twigs, leaves, stones, etc., while web-building spiders may have a shaded retreat associated with the web. In both cases, these spiders still have access to prey when in shade and can continue to hunt. This option of behavioral thermoregulation (shuttling between sun and shade) may not be available to flower-dwelling thomisids if the spiders are to maintain access to prey. Because *M. asperatus* and *M. formosipes* do not strike at prey unless it approaches within a few millimeters of the spider's chelicerae

(pers. obs.), spiders must remain near the anthers and/or nectaries in order to have access to prey. In the open field habitats where *M. asperatus* and *M. formosipes* are typically found, the upper surfaces of flowers, where the anthers and nectaries are located, are generally sun-exposed. Thus flower-dwelling thomisids may be faced with a trade-off between maintaining access to prey and avoiding high thermal stress.

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PARAPHYLY OF THE *ENOPLOGNATHA OVATA* GROUP (ARANEAE, THERIDIIDAE) BASED ON DNA SEQUENCES

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ABSTRACT: Five species of *Enoplognatha* Pavesi 1880 were recently recognized as a monophyletic *Enoplognatha ovata* group based on morphological data. We analyzed the *E. ovata* clade for monophyly using four species in the *E. ovata* group (*E. ovata* (Clerck 1757), *E. latimana* Hippa & Oksala 1982, *E. margarita* Yaginuma 1964 and *E. afrodite* Hippa & Oksala 1983) and three other closely related taxa (*E. japonica* Bösenberg & Strand 1906, *E. thoracica* (Hahn 1833), and *E. intrepida* Sørensen 1898). Two species of the presumed sister genus (*Steatoda* Sundevall 1833) were employed as outgroups. The results indicate that the “*E. ovata* clade” is not monophyletic.

The genus *Enoplognatha* Pavesi 1880 is characterized by the presence of a large colulus, a plesiomorphic character for the family; and accordingly, the genus is generally considered one of the more primitive groups in the Theridiidae. The spiders are medium-to-large sized with a subspherical abdomen. Females have a tooth on the posterior margin of the chelicerae; males usually have enlarged chelicerae, with enlarged teeth on the posterior margin, and have the paracymbium on the margin of the cymbium. The genus is very close to *Steatoda* Sundevall 1833, medium-to-large sized spiders, again characterized by a very large colulus (Levi 1962; Levy & Amitai 1981). The chelicerae are often enlarged in males, and have one or more teeth on the anterior margin, none on the posterior margin.

Enoplognatha is well known because of the striking color and pattern polymorphism exhibited by representative species in the genus, which has been most intensively studied in *E. ovata* (Clerck 1757). Three distinct morphs have been described in *E. ovata* (Locket & Millidge 1951; Hippa & Oksala 1979; Oxford 1976): *lineata* (all yellow), *redimita* (yellow with two dorsolateral carmine stripes on the abdomen), and *ovata* (yellow with a solid shield of carmine on the dorsal surface of the abdomen). The color pattern variation in *E. ovata* is genetically determined, and has been the subject of numerous studies on the genetics and evolution of the color polymorphism

(Hippa & Oksala 1979, 1981; Oxford 1983, 1985, 1989, 1991, 1992; Oxford & Reillo 1993; Reillo & Wise 1988a, b). Consistent with most invertebrate color polymorphisms (Haldane 1939) the dominance hierarchy of the expression of morphs in *E. ovata* follows the inverse of morph frequencies in nature, i.e., the least dominant (or most recessive) allele is most frequent; the most dominant is the rarest. For the mode of inheritance of the polymorphism in *E. ovata*, Oxford (1983) has proposed a two locus model: one locus is concerned with pattern and color, the other with the regulation of this color locus during development. When red-pigmented alleles are linked to the late developing allele, the color morphs are sex-limited: males are *lineata* no matter which allele they carry. *Enoplognatha latimana* Hippa & Oksala 1982 shares color, regulatory, and black spotting polymorphisms with *E. ovata* (Oxford 1992), although *E. latimana* lacks the *ovata* color morph.

In the 1980s Hippa & Oksala (1982) erected the *E. ovata* group to include *E. ovata* sensu stricto, *E. latimana*, and *E. penelope* Hippa & Oksala 1982. Members of the group share the following characters: trichobothrium on the first metatarsus subapical; elongated, sclerotized and subtubular tip of conductor in male palp; female vulva with massive copulatory pockets and abdomen with sharply delimited dorsolateral black spots (Hippa & Oksala 1982). Further examination of material

from Europe and Japan added another two species to the *E. ovata* group (Hippa & Oksala 1983): *E. afrodite* Hippa & Oksala 1983 and *E. margarita* Yaginuma 1964. *E. margarita* shares the subapical trichobothria and sclerotized subtubular tip of the conductor with *E. ovata*, *E. latimana* and *E. penelope*. However, it lacks the massive copulatory pockets. Considering all of these characters as synapomorphies, Hippa & Oksala (1983) hypothesized that *E. margarita* was the closest sister to (*E. ovata* + *E. latimana* + *E. penelope*). *Enoplognatha afrodite* has a similar body shape, ground color and spotting pattern to (*E. ovata* + *E. latimana* + *E. margarita*) but lacks these synapomorphies. Accordingly, Hippa & Oksala considered *E. afrodite* as the most ancestral species in the group.

More recently, Oxford & Reillo (1994) questioned the phylogeny of the *E. ovata* group proposed by Hippa & Oksala. Their concern arose because *E. ovata*, *E. latimana*, *E. penelope* and *E. afrodite* all have European distributions (although the former two have been introduced into North America). All occur in the Mediterranean region; but only *E. latimana* and *E. ovata* occur further north, with *E. ovata* alone extending well into northern Europe. Based on this distributional information, Oxford & Reillo hypothesized a possible Mediterranean origin of the *E. ovata* group, suggesting that the Asian *E. margarita* may have been phylogenetically misplaced by Hippa & Oksala. Indeed, the phylogeny presented by Hippa & Oksala was open to criticism because of the lack of a suitable outgroup for character polarization, few (only nine) characters used, and because there was no quantitative assessment of phylogeny.

In the current study we examined four species in the *E. ovata* group, and three other species of *Enoplognatha*: *E. japonica* Bösenberg & Strand 1906 from Japan, *E. thoracica* (Hahn 1833) from England, and *E. intrepida* Sørensen 1898 from North America. As outgroups in the analysis we used two species of *Steatoda*: *S. grossa* (C.L. Koch 1838) and *S. bipunctata* (Linnaeus 1758). We examined the pattern of sequence evolution in the *E. ovata* group to ascertain the monophyly of the clade. In this way we can evaluate the hypothesis that the Mediterranean served as the center of origin for the group as suggested by Oxford & Reillo (1994).

METHODS

Spiders sequenced.—*Enoplognatha*: *E. ovata*, two individuals from two localities: Grimes Graves, Norfolk, U.K., collected by G.S. Oxford, June 1991; and Berceto, Italy, collected by G.S. Oxford & P.R. Reillo, August 1991. *E. latimana*, one individual: Grimes Graves, Norfolk, U.K., collected by G.S. Oxford, June 1991. *E. afrodite*, one individual: near Carcassonne, S. France, collected by S. Peet, July 1988. *E. margarita*, one individual: Nukabira, Kamishihoro-cho, Hokkaido, Japan, collected by M. Matsuda, August 1992. Other *Enoplognatha* species examined: *E. japonica*, one individual: Hokkaido, Japan, collected by M. Matsuda, July 1989; *E. thoracica*, one individual: Flatford Mill, Suffolk, U.K., collected by C.J. Smith, May 1978; *E. intrepida*, one individual: Third Hill Mountain, Berkeley County, West Virginia, USA, collected by P.J. Martinat, May 1986 (det. D.T. Jennings, deposited in Smithsonian, Museum of Natural History). We also extracted DNA from *E. penelope*, one individual: Sami, Kefallinia, Greece, collected by J. Murphy, May 1987. However, we were not successful in amplifying the product. Outgroups: We used two species of *Steatoda* as the outgroup: *Steatoda grossa*: Molokai, Hawaii, collected by A.-M. Tan & G.S. Oxford October 1993 and *S. bipunctata*: Yorkshire, U.K., collected by G.S. Oxford, January 1994. Voucher specimens for all species used are at the Center for Conservation Research and Training, University of Hawaii.

DNA extraction and sequencing.—DNA samples were prepared by the conventional SDS-NaCl-Ethanol method (Medrano et al. 1990; Tan & Orrego 1992). Tissues from the legs or prosoma were placed in a 1.5 ml tube and ground with a pipette tip. After adding 15 µl of proteinase K, the tissues were incubated at 55 °C overnight. Proteins were removed by salt precipitation. DNA was precipitated, washed in alcohol and preserved in 1× TE buffer (pH 8.0).

For both double and single stranded PCR amplification we used the following primers (Table 1): E and B2 for the less variable region of the 18S sequence; B and P for the more variable region of the 18S sequence; A and B2 for the 16S sequence. PCR amplification of double-stranded products was per-

Table 1.—Primers used. Position obtained refers to *Drosophila* (Clary & Wolstenholme 1985).

Gene primer	Primer sequence in <i>Drosophila</i>	Position obtained	# Base pairs	Reference
18S E	CTGGTTGATCCTGCCAGTAG	24–553	529	modified from
18S B2	GCTGGCACCAGACTTGCCCTCC			Hillis & Dixon 1991
18S B	TTCCAGCTCCAATAGCGTAT	606–916	325	W.C. Wheeler & C. Hayashi,
18S P	GTCTTGCGACGGTCCAAGA			pers. comm.
16S A	CGCCTGTTTATCAAAAACAT	12864–13417	450	S.R. Palumbi & T. Hsiao,
16S B2	CTCCGGTTTGAAC TCAGATCA			pers. comm.

formed in 12.5 μ l volume with 38 cycles using *Thermus aquaticus* DNA polymerase (Saiki et al. 1985). Amplification was done with the following profile: 93 °C, 50 °C and 72 °C each for 30 seconds. Single strand products were prepared by asymmetric PCR (Gyllenstein & Erlich 1988) with 1:50 primer ratios in 50 μ l volumes and the same reaction profiles as above. The products were assessed by mini-gel electrophoresis using 5 μ l aliquots, and washed in sterilized distilled water with three cycles of dialysis using Millipore MC 30 (Amicon Corp.). Dideoxy chain termination sequencing (Sanger et al. 1977) was performed using the US Biochemicals Sequenase version 2.0 kit and ³⁵S labeled dATP. Negative controls were used in all PCR amplifications to make sure the sequences were not from contaminated sources. Sequences were confirmed by resequencing the same strand from another PCR product.

Phylogenetic analysis.—Ribosomal sequences were initially aligned using the program SeqEd 1.0.3 (Applied Biosystems 1995), after which alignment of multiple sequences was optimized in CLUSTAL W 1.4 (Higgins & Sharp 1988) in SeqPup 0.6 (Gilbert 1996). The entire first sequence is optimally aligned with the second entire sequence, with mismatches, gaps and insertions penalized equally, and with an additional gap length penalty for each residue in the insertion. Subsequent detailed alignment was by eye using the secondary structures (Kjer et al. 1994). The 18S sequences were aligned against the secondary structure of *Eurypelma californica* to match multiple sequences against conserved regions (Hendriks et al. 1988). The 16S sequences were aligned against *Drosophila yakuba* (Clary & Wolstenholme 1985), using the secondary structure of the region. Sequences were first analyzed using Maximum Likeli-

hood (ML) in PHYLIP (version 3.5c, Felsenstein 1993), using a generalized Jukes & Cantor (1969) model to allow for unequal base frequencies (Felsenstein 1981) as well as different rates of transitions and transversions. Sequences were also analyzed by Maximum Parsimony (MP) in PAUP (version 3.1.1, Swofford 1993). In both analyses gaps were treated as missing data. Bootstrap analyses (Felsenstein 1985) were used to estimate the statistical confidence of the different nodes in the trees.

RESULTS

The aligned sequences of the 18S region (Fig. 1) and 16S region (Fig. 2) are shown for each species (the two specimens of *E. ovata* were identical in sequence). Except for *E. thoracica* (18S only) and *E. intrepida* (16S only) we obtained 18S and 16S sequence for all species used. The data were first analyzed separately to determine the degree of congruence. The 18S sequences showed little bias in base composition, and no evidence for a transition: transversion (TS:TV) bias. The ML tree (using a TS:TV ratio of 1:1) was similar to the MP tree (using a branch-and-bound search) (Fig. 3A): (*E. thoracica* + *E. margarita*) and (*E. latimana* + *E. ovata*) were both discrete clades, and *E. japonica* fell outside all other species of *Enoplognatha*. The only difference between the analyses was that *E. afrodite* was placed with (*E. thoracica* + *E. margarita*) in the ML tree, while its position relative to (*E. thoracica* + *E. margarita*) and (*E. latimana* + *E. ovata*) was unresolved in the MP tree. Constraining *E. ovata*, *E. latimana*, *E. margarita* and *E. afrodite* to be monophyletic increased the length of the MP tree by two steps. We tested the monophyly of *E. ovata*, *E. latimana*, *E. margarita* and *E. afrodite* by calculating likelihood values (Fel-

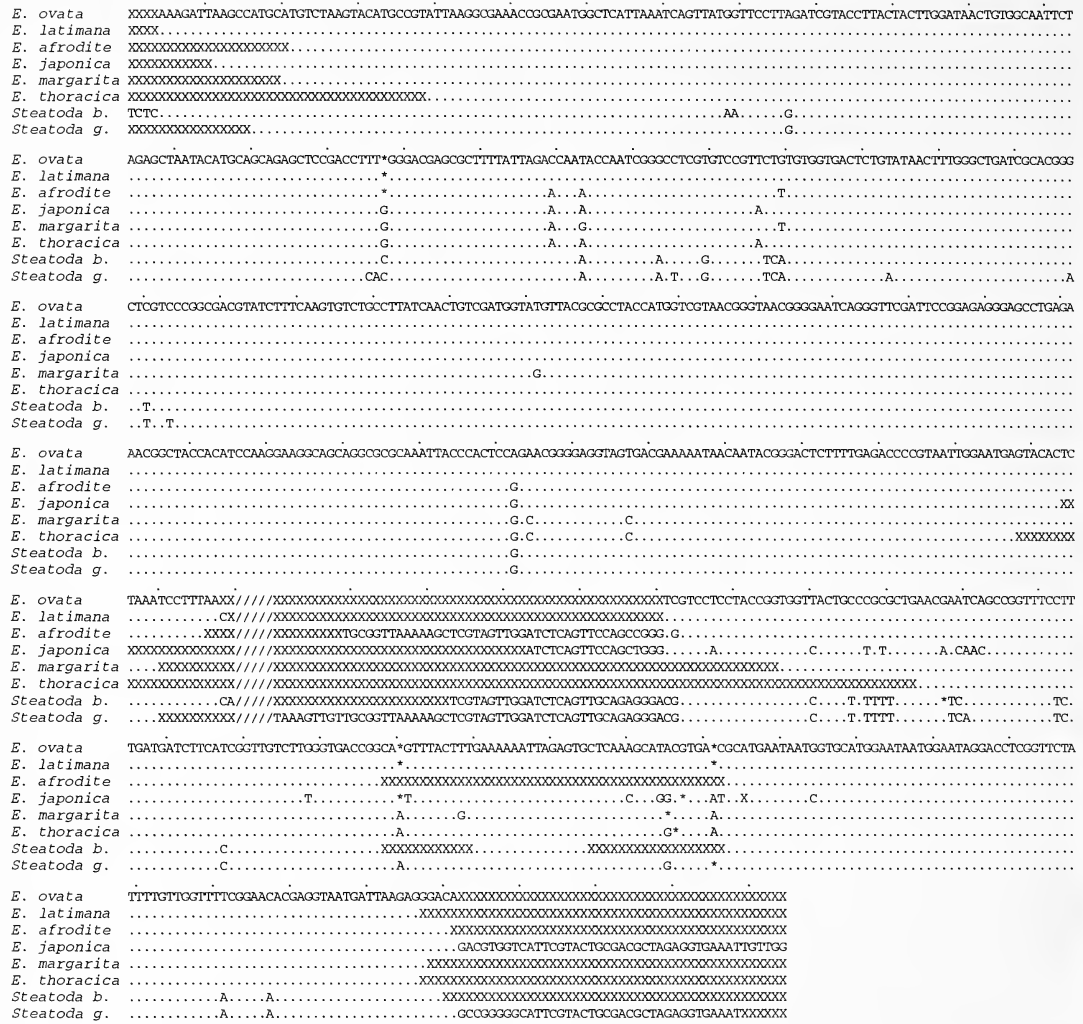


Figure 1.—Comparison of nuclear 18S ribosomal DNA sequences from 6 species of *Enoplognatha* and *Steatoda bipunctata* and *S. grossa*. Dots represent positions that are identical in sequence to the top sequence; asterisks represent gaps in the sequence required to maximize alignment; crosses indicate no data for a region. The sequence begins at position 24 in *Drosophila* and ends at position 916. The area marked by //// indicates the end of the more conserved region of the 18S sequence (position 553 in *Drosophila*) and the beginning of the more variable region (position 606 in *Drosophila*).

senstein 1988) for phylogenies that forced these taxa to be monophyletic: PHYLIP was used to perform a statistical test of each of these trees against the one with highest likelihood. This test uses the mean and variance of log-likelihood differences between trees, taken across sites (Kishino & Hasegawa 1989); trees are considered significantly different if their means differ by more than 1.96 standard deviations. The log likelihood value for the best tree was -1574.9, and was not significantly higher than the value obtained

when *E. ovata*, *E. latimana*, *E. margarita* and *E. afrodite* were constrained to be monophyletic (log likelihood -1577.8). The 16S sequences show a heavy AT bias, and accordingly most of the changes were A<->T transversions. The ML analysis was based on a model which uses the empirical frequencies of the bases observed in the input sequences, and thus accommodates biases in AT richness. Using TS:TV ratios of 1:1 and 2:1 we obtained a tree which was similar to that from MP analysis (Fig. 3B): (*E. latimana*

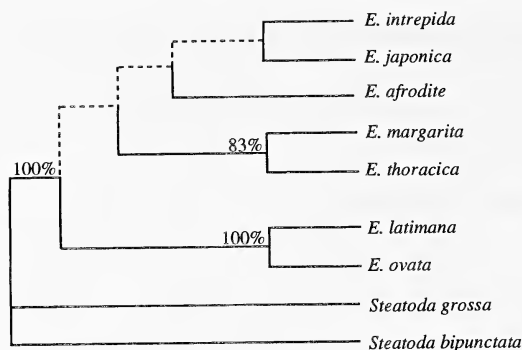


Figure 4.—Phylogeny of representatives of the genus *Enoplognatha* based on Maximum Likelihood using the combined data set of 16S and 18S sequences. All branches are significant (approximate LRT, Felsenstein 1993). Parsimony analysis gave a similar topology but with less resolution: branches that were not supported by Maximum Parsimony are indicated as dashed lines; for branches that were supported, bootstrap values are given above nodes.

+ *E. ovata*) and (*E. japonica*, *E. intrepida* and *E. afrodite*) formed discrete clades. The primary difference between the analyses was that *E. margarita* was placed with (*E. japonica*, *E. intrepida* and *E. afrodite*) on the ML tree, but with (*E. latimana* + *E. ovata*) on the MP tree. Constraining *E. ovata*, *E. latimana*, *E. margarita* and *E. afrodite* to be monophyletic increased the length of the MP tree by six steps and resulted in a significantly lower log likelihood value for the ML tree (−1491.8 for the best tree, −1518.1 for the constrained tree).

Because the results from the two data sets were largely in agreement the data sets were combined and analyzed together. The resulting ML tree differed from the MP tree only in the degree of resolution it provided (Fig. 4). In all analyses *E. ovata* fell with *E. latimana*, *E. intrepida* with *E. japonica* (and in most cases with *E. afrodite*), *E. margarita* with *E. thoracica*. The *E. ovata* + *E. latimana* clade fell outside all others. We concluded that *E. ovata*, *E. latimana*, *E. margarita* and *E. afrodite* are not monophyletic, and again tested the robustness of these conclusions. Constraining *E. ovata*, *E. latimana*, *E. margarita* and *E. afrodite* to be monophyletic increased the length of the MP tree by three steps and gave a significantly lower log likelihood value for the ML tree (−3244.9 for the best tree, −3290.5 for the constrained tree).

DISCUSSION

The species *E. latimana*, *E. penelope*, *E. afrodite*, and *E. margarita* are similar in gross morphology to the well-studied *E. ovata*, and this similarity appears to be the basis for grouping these species into what has been considered to be a monophyletic clade (Hippha & Oksala 1983). The phylogenetic analysis presented here based on both the 16S and 18S sequences does not support monophyly of the “*E. ovata* group” as described by Hippha & Oksala (1983).

The *E. latimana* + *E. ovata* clade is strongly supported, and is consistent with evidence from color polymorphism: *E. ovata* and *E. latimana* share color, regulatory, and black spotting polymorphisms (Oxford 1992), although the latter species lacks the *ovata* color morph. These genetic traits suggest a recent common ancestor for this species pair. Color polymorphism has never been reported in any other species in the “*E. ovata* group”. However, the 18S and 16S data sets individually and combined consistently place *E. afrodite* and *E. margarita* outside the *E. latimana* + *E. ovata* clade, more closely associated with *E. japonica* and *E. intrepida*, and *E. thoracica* respectively. We have no molecular sequence data from *E. penelope*, and therefore cannot evaluate its position relative to others in the “*E. ovata* group”.

The results do not refute the Mediterranean center of origin hypothesis of Oxford & Reillo (1994), although the lack of monophyly of the group indicated by the current results demands a considerably larger representation from the genus be surveyed before their origin can be identified with any degree of certainty.

ACKNOWLEDGMENTS

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CHEAP TRANSPORT FOR FISHING SPIDERS (ARANEAE, PISAURIDAE): THE PHYSICS OF SAILING ON THE WATER SURFACE

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ABSTRACT. Many pisaurid spiders inhabit the edges of bodies of fresh water and actively propel themselves across the water surface using both rowing and galloping gaits. They also sail across the water, taking advantage of the wind and their nearly frictionless interaction with the water surface. The physical interactions of *Dolomedes triton* (Walckenaer 1837) (Araneae, Pisauridae) with moving air, in a wind tunnel in which the floor was water, formed the core of the present investigation. Spiders in an elevated (sailing) posture were subjected to greater drag forces attributable to air motion than were spiders in a prone (non-sailing) posture and therefore were transported substantially faster than prone spiders. In the context of transport velocity, the benefit of adopting an elevated posture was substantially greater (relative to mass) for small spiders than for large ones, although even under the relatively steady flow conditions of the wind tunnel the velocities of the small spiders in the elevated posture were more variable than either small prone spiders or large spiders. The efficacy of adopting an elevated posture was a consequence of the steep air velocity gradient that existed above the surface of the water in the wind tunnel and that also exists above any pond over which the air is moving. Taken as a whole, the data indicate that sailing is a remarkably cheap form of transportation for *Dolomedes*, but that, at least at the edges of large bodies of water, it involves risks because it is directionally uncontrolled.

Locomotion by spiders includes ordinary terrestrial modes such as walking, running, and jumping, and quite unusual modes of air-borne and aquatic locomotion. Although the eight-legged stepping patterns of spiders on land obviously differ in detail from those of insects (Cocatre-Zilgien & Delcomyn 1993), the biomechanics of terrestrial locomotion by insects and by spiders probably differ little because they share size (Price 1984; Pennycuik 1992), exoskeletal architecture, and important aspects of the nervous system (Osorio et al. 1995, 1997). Consequently, the rich literature on the biomechanics of terrestrial locomotion in insects (e.g., Full & Tu 1990; Full et al. 1995) contributes substantially to our understanding of terrestrial locomotion in spiders. The same cannot be said of the biomechanics of aerial dispersal via ballooning and of locomotion on the water surface, forms of spider locomotion that are shared by only a few insects (ballooning: McManus & Mason 1983; Cox & Potter 1986; aquatic locomotion: Andersen 1976). For these unusual modes of locomotion, most of our knowledge of the physics and biomechanics comes from the lit-

erature on arachnids (ballooning: Humphrey 1987; Suter 1991, 1992; aquatic locomotion: Suter et al. 1997; Suter 1999a).

Fishing spiders, *Dolomedes triton* (Walckenaer 1837) (Pisauridae), the subjects of this paper, actively propel themselves across the water surface using two distinct gaits: rowing propels the spiders horizontally at velocities < 0.27 m/sec (McAlister 1959; Shultz 1987; Suter et al. 1997) and galloping, used by these spiders during some kinds of prey-capture (Gorb & Barth 1994) and during escape from predators (Suter unpubl. data), propels the spiders at horizontal velocities up to 0.75 m/sec (Suter 1999a). In both rowing and galloping, the spider accelerates forward by rapidly moving its propulsive legs backwards, transferring momentum to the water through the generation of drag. These active aquatic gaits are distinct from the alternating tetrapod locomotion used by the spiders on solid substrate (Barnes & Barth 1991; Shultz 1987).

Fishing spiders also move across the water surface propelled by air movements. Deshefy (1981) reported on one distinctive form of this "sailing" in which the spider extends and el-

evates its most anterior pair of legs, taking advantage of the increased wind speed 2–3 cm above the water surface. I have observed a second distinctive form of sailing in pisaurid spiders, in which the spider extends and depresses all of its legs, thereby raising its body well above the water surface and allowing the body and proximal leg segments to interact with more rapidly moving air currents. What follows are analyses of (1) the wind velocity gradient in the boundary layer above a pond's surface, (2) the drag forces acting on elevated vs. prone spiders, and (3) the velocity changes that result from modification of posture during sailing.

METHODS

Pond measurements.—I used a hot-wire anemometer (Thermonetics Corporation model HWA-103) to measure wind speed just above the surface of a pond at The Rockefeller University Field Research Center, Millbrook, Dutchess County, New York. At the time and location of the data collection, the water surface was upwind of the pond's usual shore but was separated from the shore by about 4 m of mud flat. I arranged the anemometer assembly (below) so that its sensor pointed upwind (away from the shore) and was over the water 0.5 m from the edge of the mud flat. As a result of the location and orientation of the sensor, it measured the speed of air that had traveled at least 120 m across the pond's surface unimpeded by structures other than the surface of the water itself. The height of the sensor above the water surface was controlled by a motorized cam which, as it rotated, raised and lowered the 0.5 m boom to which the sensor was attached. The resulting motion of the sensor tip was vertical (in space) and sinusoidal (in time), with a period of 4.3 sec, an excursion from 0.5 to 8.9 cm, and a maximum velocity of 0.06 m/sec (a small fraction of the recorded air velocities).

Analog signals from the anemometer were digitized at 10 Hz by an analog-to-digital (A/D) converter (Vernier Software Co., model ULI 5.0) under the control of data logging software (Vernier Software Co., Logger 3.04) running on a laptop computer (Apple Corporation, model PowerBook 5300c). Power for the computer was supplied by its inboard battery and power for the motorized cam and A/

D converter was supplied by a 12 V lead-acid battery.

The analysis of air speed as a function of distance to the water surface was complicated by the high variability in wind speed, presumably due to turbulence, at any single height. Although the mainstream velocity (*sensu* Denny 1993) was unknown for the data collected at the pond, the air's velocity in the boundary layer above the water must decrease to zero as height approaches zero (Denny 1993). Accordingly, I used logarithmic curve fits to characterize the relationship between height and velocity both for the pond data and for the wind tunnel data (below).

Spiders.—The adult *Dolomedes triton* (Araneae, Pisauridae) used in these experiments were collected from small ponds in Mississippi, and the juvenile was the progeny of one of the field-caught females. All were held in my laboratory under conditions described elsewhere (Suter et al. 1997).

In the experiments described below, I investigated the motion of, and the forces acting upon, killed and dried spiders of two sizes. A third-instar juvenile that had been in the lab since hatching (wet mass 0.013 g, 0.126 mN) and two adult males of approximately the same size (0.186 g, 1.82 mN; 0.243 g, 2.38 mN) were anaesthetized with CO₂ and killed by freezing. After post-mortem thawing, the spiders were immobilized in a prone posture (the juvenile and one adult) or an elevated posture (the second adult) and allowed to air dry for several weeks. During the weeks of experimentation, the postures of the adult spiders (Fig. 1) remained unchanged. During measurements of horizontal velocity, however, the posture of the juvenile was changed from prone to elevated to make possible direct comparisons of the same spider in two postures: to accomplish the posture change, I softened the spider's most proximal leg joints by moistening them, and then repositioned the limbs and air dried the spider for several days.

The weights of the dried adult spiders (elevated, 0.736 mN; prone, 0.959 mN) were matched more closely by fastening with epoxy a small, flat coil of nichrome wire (0.221 mN) to the dorsal surface of the cephalothorax of the spider in the elevated posture. The adult spiders then both had weights of 0.96 mN. Temporary weight modifications were accomplished by hanging the same short length of

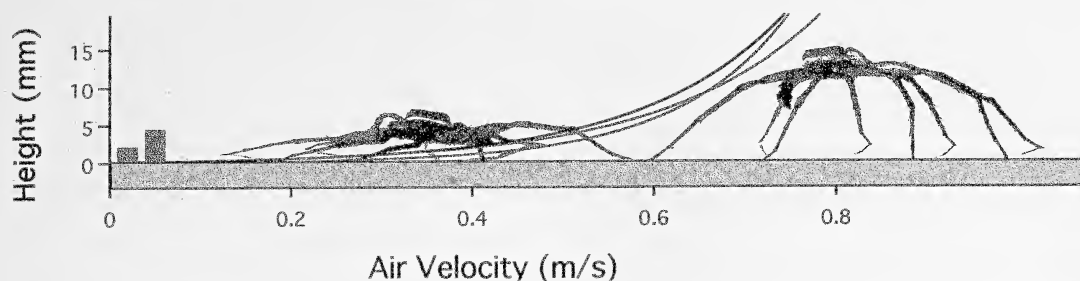


Figure 1.—Adult spider postures as digitized from photographs of the large dried spiders used in the experiments reported here. For comparison, the small spider in the prone and elevated postures had heights of 2.1 mm and 4.4 mm respectively (filled bars at left). A spider in the prone posture (left) is exposed to lower horizontal air velocities than is a spider in the elevated posture (right). The three curves are the same as those shown in Figure 5, but with the axes reversed.

30-gauge copper wire over the cephalothorax of each of the adult spiders. All experiments with the dried spiders were conducted at laboratory temperatures between 20–23 °C.

Wind tunnel measurements.—The horizontal wind tunnel used in this study had an experimental chamber measuring $20 \times 20 \times 87$ cm (length). The floor of the chamber had a 0.6 cm deep cavity beginning 36 cm downwind from the air inlet and having horizontal dimensions of 18×40 cm. When the cavity was filled with water, the surface of the water and the surface of the remainder of the floor of the experimental chamber formed an unbroken, flat surface. Both ends of the experimental chamber were fitted with 2 cm thick furnace filter fiber to suppress turbulence. With the exception of the filter, the upwind end of the tunnel was open to room air. Ten cm beyond the filter at the downwind end of the tunnel the air entered a 10.1 cm (diameter) polyvinyl chloride (PVC) pipe on the end of which was mounted a small fan oriented so that it pulled air through the tunnel. Although valving in the pipe leading to the fan allowed me to control air speed in the experimental chamber, I conducted all tests at a nominal air speed of 0.65 m/sec (measured at the center of the air stream, 52 cm from the upwind end of the experimental chamber).

I used a hot-wire anemometer (Thermonetics Corporation, model HWA-103) to monitor air velocity in the chamber and to measure the airspeed profile as a function of the distance from the water surface. The 5 mm (diameter) anemometer probe was inserted through a 6 mm (diameter) hole in the top of the experimental chamber, 52 cm from its upwind end.

A micromanipulator, mounted on the outside of the chamber, facilitated adjustment of the position of the anemometer's sensor relative to the water surface.

At the beginning of a sailing trial, a dried spider was placed gently on the water surface approximately 42 cm from the upwind end of the chamber (6 cm from the upwind edge of the water surface) and at the side-to-side center of the water surface. The spider was held at that location by a pair of nichrome wires assembled in an inverted "V" and attached to a probe that could be raised several cm, releasing the spider. The spider was released only after the tunnel fan was turned on and the chamber had reached a constant nominal velocity of 0.65 m/sec. To measure the sailing velocity of a dried spider, I recorded its location in the horizontal plane, beginning when the spider crossed a line 2.5 cm downwind from its release site, using an SVHS video camera (Panasonic model AG-455) and Image (National Institutes of Health software, version 1.55 f) as a frame grabber and image digitizer (at a rate of 20 frames per second). I digitized the location of the center of the spider's cephalothorax using tools resident in Image, and then calculated velocity as the distance moved divided by the frame interval.

I used a horizontal balance (Suter et al. 1997) to measure horizontal drag forces on the adult dried spiders in the wind tunnel. The balance employed an electronic clinometer (Applied Geomechanics Inc. model 900 Bi-axial Clinometer) with a resolution of 0.01° (1.75×10^{-4} rad) to measure small angular displacements that were directly proportional to the horizontal force applied to the spider.

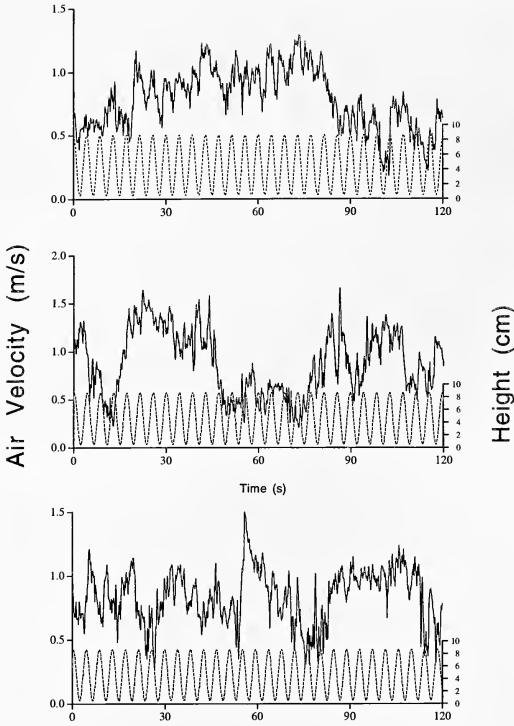


Figure 2.—The horizontal wind speed (solid line) within the 10 cm deep layer of air just above the surface of a pond varied significantly with height of the sensor (dashed line) in each case although the effect was small ($0.04 < r^2 < 0.12$, $P < 0.05$). The residual variability is assumed to be a consequence of the turbulence in the air.

The end of the vertical arm of the balance consisted of a pair of nichrome wires assembled in an inverted “V” which immobilized the spiders without applying any vertical force to them. Clinometer output (in volts) was digitized by an A/D converter (National Instruments Corporation, model NB-MIO-16L) driven by a LabView 3 program (National Instruments) on an Apple microcomputer (Power Macintosh 7100/80AV).

RESULTS

Pond and wind tunnel air movement.—Velocity measurements of the air within 10 cm of the surface of the pond (V_p) indicated that the air was turbulent, with large fluctuations in velocity at several scales (Fig. 2). Only a small amount of the variability in V_p could be attributed to the changes in the position of the anemometer’s sensor ($0.04 < r^2 < 0.12$), although the small effect of the

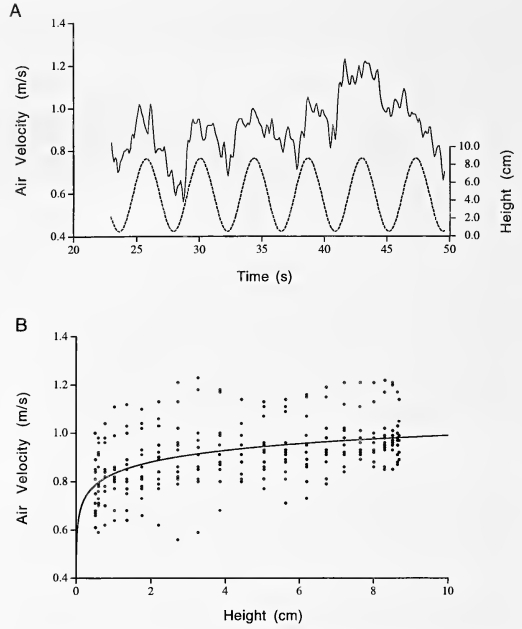


Figure 3.—During a period of relatively constant average wind velocity (23 sec to 50 sec in top graph of Figure 2), velocity of the air just above the pond’s surface (A, V_p) varied approximately as the \log_{10} of height (B, assuming, as is required by boundary layer physics, that V_p at the surface must be zero; $V_p = 0.16 \log_{10} \text{height} + 0.83$, $r^2 = 0.225$, $n = 267$, $P = 0.0001$).

height of the sensor was significant ($P < 0.05$ in each sample in Fig. 2). For a subsample of velocity data in which large-scale fluctuations in V_p were relatively small, the influence of sensor height was more prominent and V_p varied approximately as the \log_{10} of height (Fig. 3). The logarithmic relationship between V_p and height can be seen most clearly during short segments of the pond data (Fig. 2) which include only a half cycle or a full cycle of the sensor and therefore do not conflate velocities that are widely separated in time (Fig. 4), and is entirely in accord with boundary layer theory (Schlichting 1979).

In the wind tunnel, constant fan velocity and suppression of some of the turbulence made the influence of height on wind tunnel velocity (V_w) much more detectable: logarithmic curve fits on three data sets indicated that sensor height explained more than 90% of the variation in V_p (Fig. 5; $0.91 < r^2 < 0.97$).

Sailing velocity and drag forces in the wind tunnel.—Images of dried spiders sailing downwind in the wind tunnel indicated that,

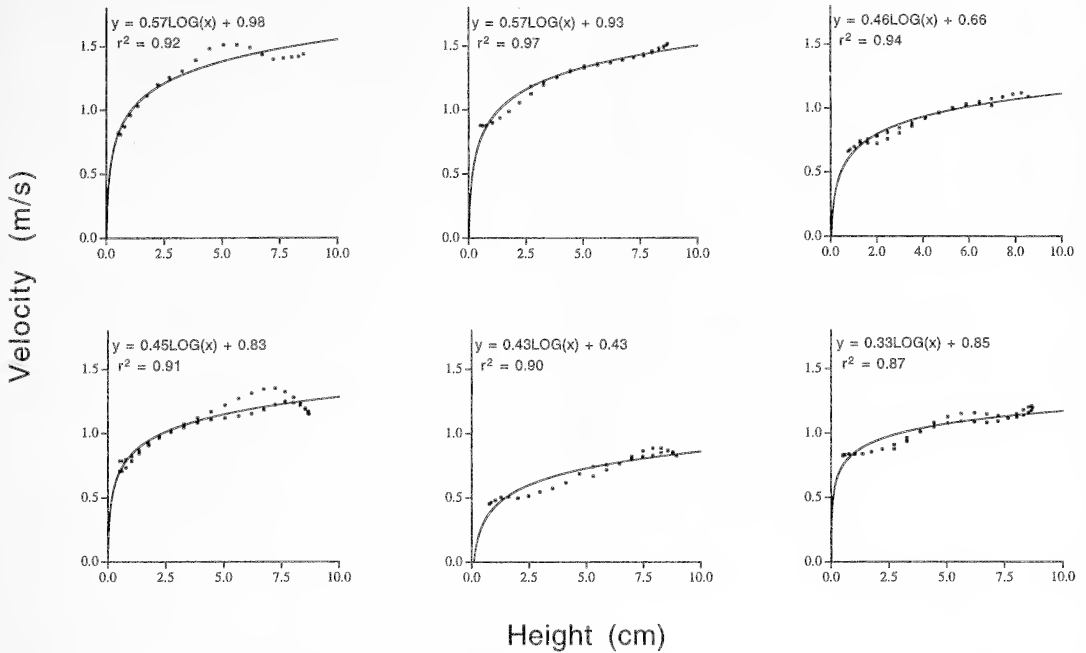


Figure 4.—The relationship between V_p and height above the water is most clearly visible during the brief periods of time (from Fig. 2) which include \leq one full cycle of the sensor and therefore do not conflate velocities that are widely separated in time. In the examples shown here, \log_{10} curve fits worked well: $0.86 < r^2 < 0.98$.

by the time each had reached the line where video digitizing began, it was moving at relatively constant velocity: thus it had reached the terminal velocity (V_t) at which the forces propelling it (air-induced drag) were in balance with the forces resisting its motion (water-induced drag). Under wind tunnel conditions, a large spider (0.42 g, wet weight) dried in an elevated posture always had greater velocities (V_t) than a similar-sized spider that had been dried in a prone posture. At the weights at which the effect of the two postures could be compared directly, being elevated conferred about a two-fold velocity advantage over being prone, but a much greater (3.7-fold) advantage accrued to the elevated form of the very small spider (0.013 g, wet weight) (Fig. 6). A stepwise multiple regression of velocity on height (a function of posture) and weight for the large spider yielded a highly significant relationship ($P < 0.01$, $F = 106.96$, adjusted $r^2 = 0.876$) in which velocity varied directly with height and inversely with weight. For the small spider, the difference between V_t for elevated and prone postures was highly significant (Mann-Whitney U test, $Z =$

-2.646 , $P = 0.008$) and the variability in V_t for the elevated small spider was much greater than that for any other group (Fig. 6). The very high variability in V_t for the elevated small spider is probably attributable to small eddies in the air stream close to the water surface that can influence very small objects but are averaged out when interacting with the much greater leg span of the larger spiders. To test for effects of horizontal orientation relative to the direction of air movement in the wind tunnel, I released dried large spiders at different horizontal orientations, with the expectation that any relationship would be approximately sinusoidal. The orientation of the large dried spiders did not have a significant influence on V_t for either the elevated or the prone spiders (Fig. 7). In direct measurements of the drag force exerted on spiders by moving air, drag on a spider in the elevated posture was significantly higher than drag on the prone spider (0.055 ± 0.002 mN vs. 0.029 ± 0.002 mN; $t = 31.4$, $P < 0.0001$) as expected from the results of dynamic tests (Fig. 6). The 1.92-fold difference between the mean values fits well with

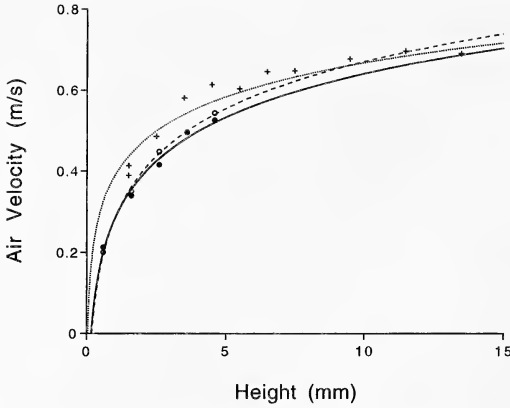


Figure 5.—In the wind tunnel, air velocity (V_w) varied with the \log_{10} of height above the surface of the water. For the three runs shown here, the equations were $V_w = 0.36 \log_{10} \text{ height} + 0.28$, $r^2 = 0.987$, $V_w = 0.39 \log_{10} \text{ height} + 0.28$, $r^2 > 0.99$, and $V_w = 0.28 \log_{10} \text{ height} + 0.39$, $r^2 = 0.920$.

the 2.12-fold differences between measurements of V_t for the identical elevated and prone spiders at their lightest weight (Fig. 6).

DISCUSSION

A fishing spider, lying prone on the surface of a pond and not anchored to floating vegetation or debris, will move passively across the water at a rate influenced by the spider's mass and the velocity of wind over the pond (Fig. 6). The actual air velocity to which the spider is exposed, however, is strongly influenced by the location of the spider's body parts relative to the water surface (Figs. 4, 5). This connection between elevation and air velocity means that the velocity at which the spider can travel under the influence of air movements is closely tied to the spider's posture (Figs. 1, 6).

Quasi-passive locomotion, like ballooning.—Although the propulsive forces involved in sailing are environmental rather than physiological, the importance of posture and the stereotyped performance of the postures employed in sailing (above and Deshefy 1981) indicate that this form of locomotion is not purely passive. On the other hand, because wind direction is not controlled by the spider and because the keel-less spider apparently has no control of its own direction relative to the wind (as do humans in sailboats), the sailing spider cannot influence its destination. In that regard, this quasi-passive form of loco-

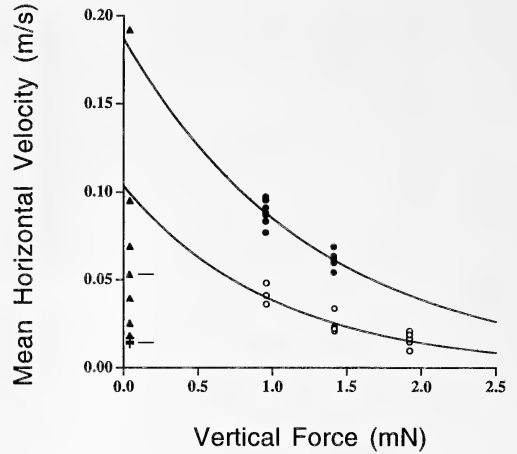


Figure 6.—During wind tunnel measurements of the horizontal terminal velocities (V_t) of sailing spiders, V_t varied with spider size as well as with mass and posture. For the large spiders (wet weight = 1.82 and 2.38 mN), the elevated posture (●) resulted in a doubling of V_t relative to V_t for the prone posture (○) (dry weight = 0.96 mN – elevated: 0.088 ± 0.007 m/sec vs. prone: 0.042 ± 0.006 m/sec, ratio = 2.12; dry weight = 1.42 mN – elevated: 0.062 ± 0.004 m/sec vs. prone: 0.024 ± 0.005 m/sec, ratio = 2.51). For the small spider (wet weight = 0.013 g), the elevated posture (▲) resulted in a 3.7-fold increase in V_t (based on comparison of medians, designated with dashes) relative to V_t for the prone posture (+). See text for statistical analyses. Exponential curves (because V_t must approach zero as vertical force becomes very large) fitted to the data for the large spiders were $0.187 F_v^{-0.342}$ (elevated, $r^2 = 0.873$) and $0.104 F_v^{-0.433}$ (prone, $r^2 = 0.766$) where F_v is the vertical force. The velocities shown here, for all but the heaviest prone spider, overestimate V_t achievable during sailing by live spiders because the dried spiders were lighter and therefore created shallower dimples and less water-generated drag (Suter 1997).

motion resembles ballooning in which, once airborne, the spider has no control over its horizontal direction and therefore little control over its destination, and in which posture is crucial (Suter 1992).

Two other parallels between sailing and ballooning are worth noting: neither requires substantial muscular input, and in both forms of locomotion, smaller individuals have substantial advantages. The energetic cost of whole-body sailing (*cf.* Deshefy 1981) can be estimated as the work needed for the spider to raise its body to an effective sailing height—for the larger spiders used as models in this

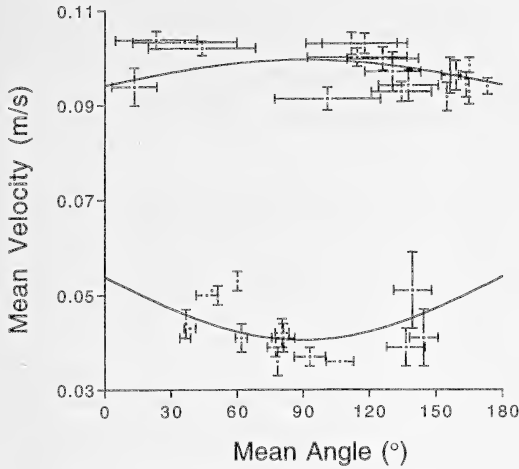


Figure 7.—Sinusoidal curve fits on the velocities of large spiders in elevated (upper) and prone (lower) postures, after release at different horizontal orientations relative to the direction of air motion in the wind tunnel, revealed that orientation had no significant effect on V_t . Each datum consists of mean \pm SD velocities and angles (relative to 0°, facing directly upwind) for one spider's motion following a single release: variation in V_t reflects measured changes in velocity between digitized frames from videotaped records; variation in angle is a consequence of the slow rotation of the released spider during its movement downwind. For the elevated posture, $V_t = 0.005 \sin(\text{angle}) + 0.094$ ($r^2 = 0.119$, $n = 19$, $P > 0.05$), and for the prone posture, $V_t = 0.013 \sin(\text{angle}) + 0.054$ ($r^2 = 0.144$, $n = 17$, $P > 0.05$).

study (live weight ~ 2.1 mN), the work required to raise the center of mass from 4–12 mm above the water is about 1.68×10^{-5} joules, an amount of work that needs to be done only once during a sailing episode. In comparison, for the smaller of the spiders used as models in this study (live weight = 0.126 mN), the cost of elevating the center of mass 2.3 mm is about 2.90×10^{-7} joules. The smaller spider's velocity in the elevated posture is approximately the same as that of the larger spider (Fig. 6), but the cost of attaining that posture for the larger spider is 58 times as great. Thus, the efficiency of sailing is far greater for very small spiders, but for any spider the cost is very small: consumption of a single fruit fly (Golley 1961) would provide sufficient energy to elevate the larger spider thousands of times! Sailing is, like ballooning (Suter 1999b), a remarkably cheap form of transport.

Risk assessment.—Fishing spiders are attacked from below by fish (G. Miller pers. commun.) and are likely also to suffer predation from above by anurans and birds. Because their predators' feature detectors undoubtedly respond to specific cues (e.g., shape, size, motion: Lettvin et al. 1959; Ewert 1974; Ewert et al. 1983) the suppression of any of these cues can result in a reduction in the probability of eliciting predation. In this context, sailing can be viewed as an inconspicuous form of locomotion that offers a relative reduction in predation risk through the suppression of visual cues: propulsive motions of the legs relative to the body are absent, and surface waves caused by rowing and galloping locomotion (Suter et al. 1997; Suter 1999a) are not generated at the velocities achieved during sailing (Fig. 6; Denny 1993; Vogel 1994).

Another kind of risk, that associated with motion whose direction is not controlled by the spider, should rise with elevated uncertainty about the ecological suitability of the destination. In the ponds usually inhabited by *D. triton*, this risk is minimal because the ultimate destination of a sailing spider will always be an edge of the pond, a location that may be unfamiliar to the spider but that is apt to be as ecologically suitable as the spider's original location. In contrast, species of *Dolomedes* that inhabit the shores of islands in the Great Lakes of North America cannot be assured of a benign destination if the wind is offshore: sailing away from a shore can take the spider into open waters where both food and cover are unavailable and where the direction of the nearest shoreline is undetectable.

Function.—For fishing spiders living at the edges of ponds, sailing is both energetically cheap and relatively safe (above). But this form of locomotion has only rarely been observed in nature and its function in the context of more controlled modes of locomotion on the water surface (Suter et al. 1997; Suter 1999a) remains unclear. Because sailing is most efficient for smaller spiders (Fig. 6) and because heavy *D. triton* are unable to elevate their bodies into rapidly moving air without exceeding the ability of the water's surface tension to support them (Suter 1999a), the primary function of sailing may be to facilitate

dispersal in young spiders, a hypothesis that is yet to be tested.

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NOTES ON THE SOCIAL STRUCTURE, LIFE CYCLE, AND BEHAVIOR OF *ANELOSIMUS RUPUNUNI*

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ABSTRACT: Observations on the colony structure, life cycle, and behavior of *Anelosimus rupununi* in eastern Ecuador point to a level of social organization similar to that of *Anelosimus eximius* and *Anelosimus domingo*, confirming its status as a non-territorial, permanently-social species. *Anelosimus rupununi* colony members were seen to cooperate in prey capture and transport, to feed communally, and to take turns in tending the egg sacs. Sex ratios were also highly female-biased. There were, however, some interesting differences with these other species. *Anelosimus rupununi* egg sacs were grouped as part of maternal care efforts, with grouped sacs being more likely to be tended than ungrouped sacs. Males and females apparently matured at the same instar, males appeared shorter-lived than females, and individuals within the nests were clearly synchronized with each other in the stage of their life cycle. Also, as would be expected from its notably smaller body size, *A. rupununi*'s life cycle appeared shorter than that of *A. eximius*.

Understanding the evolution of animal social systems often requires exploring within a comparative framework both the environmental conditions that may have selected for social living and the suite of traits that in particular phylogenetic lineages may have facilitated or hindered the transition from one level of social organization to another (Crespi & Choe 1997). Spiders appear ideal for this exploration because they have given rise to several independent derivations of complex social behavior involving cooperation in nest building, prey capture, feeding, and brood care (for a recent review, see Avilés 1997). Additionally, the genera that contain these cooperative species—also known as “non-territorial permanent social” or “quasisocial”—contain species with other levels of social organization. The genus *Anelosimus* Simon 1891 (Araneae, Theridiidae) in America, in particular, includes at least four non-territorial permanent-social species, which are mostly tropical, and several periodic-social or solitary species that inhabit both tropical and temperate areas of the New World (Levi 1956, 1963, 1972; but see Furey 1998). Among these, only the permanent-social *Anelosimus eximius* Keyserling 1884 has been relatively well studied (see references cited in Avilés 1997). Other species have received comparatively little attention (see Brach 1977; Fowler & Levi

1979; Nentwig & Christenson 1986; Smith 1987; Rypstra & Tiley 1989; Avilés & Maddison 1991; Furey 1998; Avilés & Gelsey 1998).

Here we present observations on the colony structure, life cycle and behavior of *Anelosimus rupununi* Levi 1956 in eastern Ecuador. This species had been previously reported from Trinidad, British Guiana, northwestern Peru, Brazil and Paraguay (Levi 1963), although the Paraguayan specimens apparently correspond to misidentified *A. lorenzo* Levi 1979 (Fowler & Levi 1979). No previous records existed from Ecuador where this study was conducted. The only published information on *A. rupununi* was a photograph of a nest (Levi 1972) and the suggestion that the species is “probably quasisocial” because it forms extensive colonies (Fowler & Levi 1979). Fowler & Levi (1979) noted that the apparently closely related *A. lorenzo* forms perennial colonies that may contain hundreds of individuals that cooperate in prey capture, feeding and brood care. Here we confirm that *A. rupununi* has a level of social organization comparable to that of the permanent-social *A. eximius* and *A. domingo* Levi 1963. We note, however, some interesting differences between *A. rupununi* and these two species. In particular, in *A. rupununi* individuals within the nests are relative-

ly well synchronized in the stage of their life cycle and group their egg sacs as part of maternal care efforts.

We discovered colonies of *A. rupununi* at two sites in eastern Ecuador, the Yasuni National Park (YNP) and the Jatun Sacha Biological Station (JSBS). The YNP (including the adjacent Waorani Reserve) comprises 1,662,000 hectares of primary rainforest. We visited the area near the confluence between the Tiputini and Tivacuno rivers (0°41'S, 76°24'W, 210–250 m elevation) where the Estación Científica Yasuní (ECY, Pontificia Universidad Católica del Ecuador) is located. The JSBS is located on the southern banks of the Upper Napo River (1°4'S, 77°36'W, 450 m) and comprises 2000 hectares of mostly primary forest surrounded by farms. At both sites we searched for colonies of *Ane-losimus* spp. both within the forest and along the forest edge. At the YNP (19–23 July 1997) we inspected 4 km inside the forest, 10 km along the Tiputini river, and 7 km along the ECY-Tibacuno road. At the JSBS (9–17 July and 3–9 August 1997 and April 1998), we inspected 6 km inside the forest, 55 km along the Arajuno, Napo, and Huambuno rivers, and 20 km along the Tena-Ahuano road. Additionally, the colonies located at the JSBS in mid-July 1997 were monitored bi-weekly until mid-February 1998 or until their extinction.

Web architecture.—We located eight nests of *A. rupununi*, all of them in forest edge or open and disturbed areas. A nest at the YNP occurred on the crown of a tree that hung over the Tiputini River. The seven nests located at the JSBS occurred on trees or bushes in farms adjacent to the preserve. We could not locate any nests in the forest interior where, in contrast, we located numerous *A. domingo* and *A. eximius* nests. The nests of *A. rupununi* differed from those of *A. eximius* in several respects: they were made of silk of a whiter and lighter appearance, contained almost no dry leaves and did not have a definite top-bottom polarity. In fact, rather than being basket-shaped, with a basal sheet and extensive silk lines extending upwards, the nests of *A. rupununi* enveloped pieces of vegetation on all sides and had only short if any lines extending upwards. This architecture may result from the location of the nests in areas with no other vegetation above. This architecture, combined

with the spatial distribution of the nests, suggests that *A. rupununi* is a forest edge or canopy species.

Individual instars.—Spiders of all instars were of a generally dark brown or black coloration that obscured the dorsal abdominal pattern characteristic of *Ane-losimus*. Based on the state of the genitalia, general size, and body proportions, we classified the later-instar spiders into “juveniles,” “subadults” and “adults.” Measurements of the tibia plus the patella of leg I yield a multimodal distribution that supports this *a priori* classification of instars (Fig. 1). Based on these data, it appears that after the last undifferentiated juvenile instar, both males and females have only one subadult instar before acquiring sexual maturity. This situation differs from that found in *A. eximius* and *A. domingo* where females are significantly larger than males as a result of having one additional subadult instar before maturing (Avilés 1986; unpubl. data). Egg sacs were subspherical in shape ($2.00 \times 2.00 \times 2.75$ mm, $n = 1$), of an off-white coloration, and tended to be bundled in groups of up to eight sacs (see below). Possibly as a camouflage mechanism, the sac bundles contained debris attached to their surface that gave them a flower like appearance. Egg sacs contained from 8–13 eggs (mean \pm SE: 10.6 ± 0.6 eggs; $n = 13$). No parasitoids were present inside the sacs examined.

Colony age structure and life cycle.—The four nests whose contents we inspected contained from a single adult female to close to 3000 spiders. The age distribution within the two largest nests (Table 1) suggested a definite synchronization in life cycle stage among individuals within a colony. When seen in July 1997, the YNP colony contained mostly adult females and egg sacs, while the JS 1 colony contained primarily subadult females and no egg sacs.

The synchronization in life cycle stages within the JS 1 colony continued throughout the period it was observed (Fig. 2). Six weeks after it was first recorded, the spiders in this colony had matured and laid their eggs. By week 10, the first spiderlings had emerged from the sacs, and by week 16 some of these spiderlings had reached the adult instar. In the mean time, the maternal females had decreased in number and were apparently all gone before their offspring reached the sub-

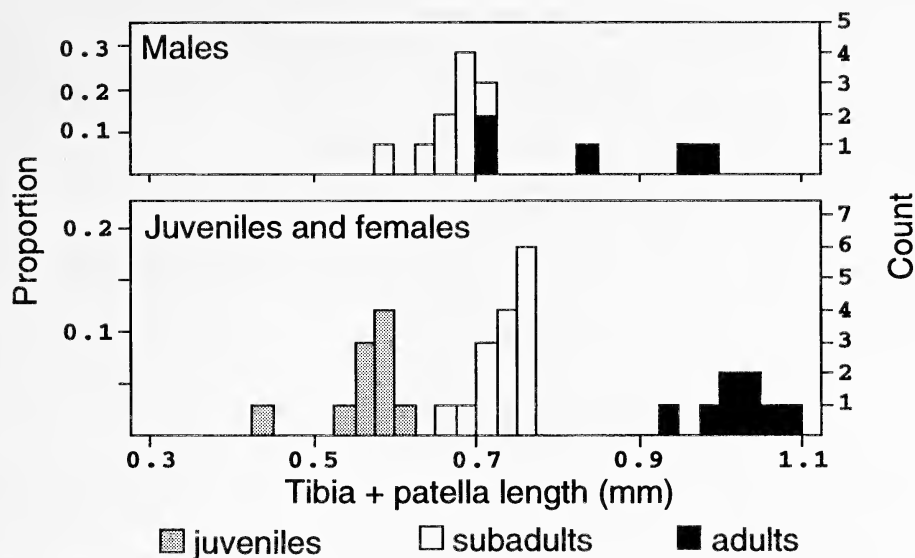


Figure 1.—Tibia + patella (leg pair I) measurements of late-instar *Anelosimus rupununi* spiders separated *a priori* into “juveniles,” “subadults,” and “adults” based on the state of their genitalia, size, and body proportions. Mean total body length (\pm SE) for the different instars and sexes are as follows: late-instar juveniles = 1.39 ± 0.03 mm; subadult females = 1.76 ± 0.02 mm; subadult males = 1.59 ± 0.05 mm; adult females = 1.81 ± 0.01 mm; adult males = 1.75 ± 0.05 mm.

adult instar. No new sacs appeared in the colony between weeks 14–18. Males appeared much shorter-lived than females, as no adult males were noted in this colony during the periods of egg sac and offspring development. Consistent with this observation, almost no males were present in the YNP colony when it contained primarily adult females and egg sacs (Table 1).

A shorter male lifespan in *A. rupununi* contrasts with the situation in *A. eximius* where males and females have adult lives of comparable length (Avilés 1986). The synchronization of life cycle stages within *A. rupununi* colonies also contrasts with the situation in *A. eximius* and *A. domingo*, where, although separate, the generations within the

colonies are less clearly distinct (Avilés pers. obs.). Strong internal synchronization of life cycle stages has also been described for other permanent-social species such as *Achaearanea wau* Levi, Lubin & Robinson 1982 (Lubin & Robinson 1982), *Stegodyphus dumicola* 1898 (Seibt and Wickler 1988), and *Aebutina binotata* Simon 1892 (Avilés in press).

During the six months following its discovery, the spiders at the JS 1 colony completed one and a half generation cycles (Fig. 2). Mature spiders of the offspring generation remained at the original site and in early December—four months after the onset of the prior egg-laying cycle—started to lay their own eggs. *Anelosimus rupununi*, therefore,

Table 1.—Size and inhabitants of *Anelosimus rupununi* nests when first seen in July 1997 at the Yasuni National Park (YNP) and the Jatun Sacha Biological Station (JS).

Colony	Nest size (cm)	% scored	Sacs	Juv.	Females		Males	
					Subad.	Adult	Subad.	Adult
YNP	88 × 45 × 12	100	244	14	5	229	0	4
JS 1	130 × 95 × 80	10	0	25	224	27	10	12
JS 2.1		100	10	present	0	7	0	0
JS 3		100	0	0	0	1	0	0

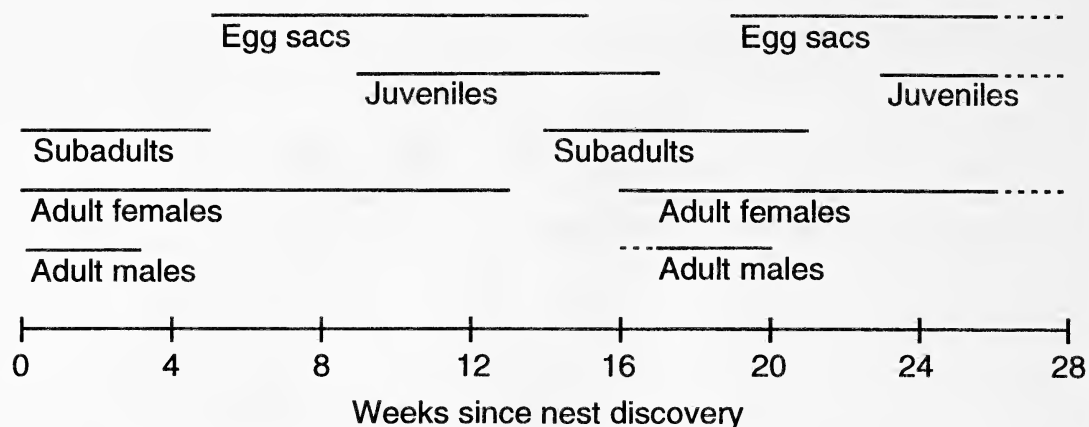


Figure 2.—Idealized life cycle of an *Anelosimus rupununi* colony based on bi-weekly inspections of a nest discovered at the Jatun Sacha Biological Station in mid-July 1997. Lines mark the presence of individuals of particular life cycle stages within the colony.

may complete three generations a year, in contrast with *A. eximius* that completes only between 2.4–2.6 generations a year at this same latitude (Avilés 1986).

Sex ratio.—We estimated the tertiary sex ratio in a colony that contained primarily subadult spiders and, thus, would not have been affected by the shorter life span of adult males (Colony JS 1, Table 1). We are assuming that the collected $\frac{1}{10}$ fraction of this colony is representative of the whole, as spiders of all instars appeared homogeneously distributed throughout the nest. The sex ratio among the 273 subadult and adult spiders in this sample was 8% males (4.7–12.5%, 95% c.i.) (Table 1). This value is strikingly similar to the 9% and 8% males reported as the sex ratio among developing embryos in *A. eximius* and *A. domingo*, respectively (Avilés & Maddison 1991).

Sacs per female.—Given the synchronization in life cycle stages within *A. rupununi* nests, the ratio of sacs to females during the peak of the egg laying period may be a reasonable representation of the number of sacs produced per female. The two colonies censused at this stage contained 1.04 and 1.40 sacs per female, respectively (Table 1). In contrast, estimates of the egg sac production in *A. eximius* that take into account its more protracted egg-laying period indicate that females in this species typically produce fewer than one sac per female (Avilés & Tufiño 1998; see also Vollrath 1986). The fecundity of *A. rupununi*, therefore, may be higher than what its

small adult female body size and small number of eggs laid per sac would lead us to suspect.

Behavior.—We conducted casual observations on prey capture and feeding in the YNP colony after it was collected whole and brought intact to the field station (the colony enveloped a stiff piece of vegetation and, thus, maintained its original shape and structure). Following the artificial introduction of prey items in the nest, we recorded two cooperative prey capture events. In one event seven spiders participated in biting and subduing a cricket that was 4–5 times larger than the individual spiders. In another event three females cooperated in moving a captured membracid towards the nest's interior. In both cases, communal feeding followed. Groups of communally feeding spiders were also observed in other colonies in the field.

A behavior not previously observed in species in the genus *Anelosimus* consisted in the bundling of the egg sacs in groups. Also in the YNP colony (see above), we observed a female in the process of completing an egg sac and attaching it to a nearby pair of bundled sacs. The egg sac was initially suspended from the web as the spider crawled around it adding to its surface silk she pulled from her spinnerets. After the sac was completed, the spider detached it and brought it towards a pre-existing pair of sacs. After attaching the sac to the pair, the spider mounted guard by the new-formed trio.

Out of the 244 sacs present in this colony

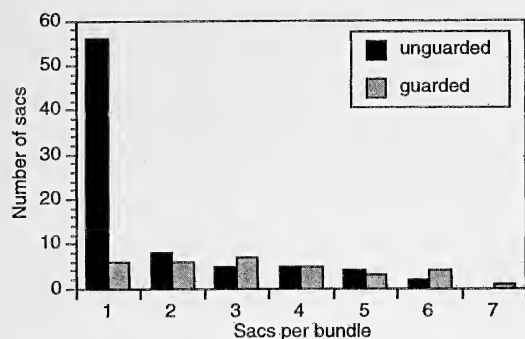


Figure 3.—Frequency distribution of guarded and unguarded egg sac bundles present in the YNP nest five days after it was collected whole.

when collected, 182 — or 75% — occurred in groups of 2–7 sacs (Fig. 3). The remaining sacs were single. When we started dissecting the colony in the laboratory five days after its collection, we noted that 31 out of the 234 females in the nest were involved in sac guarding. However, 105 of the 244 sacs were being guarded as grouped sacs were significantly more likely to be tended than ungrouped sacs (median number of sacs per bundle among guarded sacs = 3, among unguarded sacs = 1; Mann-Whitney $U = 1975$, $P < 0.0001$) (Fig. 3). Usually a single female mounted guard by each sac bundle, apparently relayed by other individuals. During a one hour observation period we noted that females repeatedly moved away from the sacs they were tending as a second female with whom they exchanged leg touches approached the area. Sac bundling was also observed in the Jatun Sacha colonies. The 10 sacs present in the JS 2.1 colony (Table 1), for instance, occurred in a group of eight and a group of two.

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MOVEMENT OF THE MALE BROWN TARANTULA, *APHONOPELMA HENTZI* (ARANEAE, THERAPHOSIDAE), USING RADIO TELEMETRY

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ABSTRACT. This study was designed to gain insight into the “migratory” life history component of the male brown tarantula, *Aphonopelma hentzi* (Girard 1854), and to determine if radio telemetry could successfully answer questions regarding the ecology of theraphosids. Tarantulas were equipped with radio transmitters and movement monitored using an antenna and radio receiver. Overall movement of males was in all directions and randomness could not be excluded as a factor. Individual males moved relatively large distances, up to 1300 m, and significant directedness was only found in three individuals. In addition, notes on habitat, ecology and behavior are presented.

Many spiders disperse over large distances by ballooning, and this is well documented in the aranemorphs (Weyman 1993, 1995; Weyman et al. 1995). Mygalomorph spiderlings have been observed ballooning over short distances (Bristowe 1939; Coyle 1983, 1985; Coyle et al. 1985); and Coyle (1983, 1985) concluded that ctenizid spiderlings could travel significant distances if they launch from taller vegetation. However, immature tarantulas (Theraphosidae) are not known to balloon. There is no mention in the literature of the large scale movement of male tarantulas. This study was designed to determine the large scale distance and direction traveled by the mature male tarantula, *Aphonopelma hentzi* (Girard 1854), using radio telemetry.

Mature males leave their burrows to search for mates from June to December (Baerg 1928, 1958; Gertsch 1979; Minch 1979a). Individual males have been observed crossing highways, appear to be moving in the same direction, and resist being redirected (Baerg 1958, 1963). Baerg (1958) stated that rarely are the movements of hundreds of individuals reported. Magnusson (1985) witnessed a coordinated movement of 89 male *Cyclosternum* sp. in Brazil. Mass movements could occur when weather conditions are ideal for travel (Baerg 1958). In addition, Baerg (1958) proposed a general “migration” of tarantulas

throughout the southwestern United States, Mexico, and possibly Panama. Baerg (1958) also suggested that reduced inbreeding could result from males moving large distances in search of mates.

Migration differs from dispersal in many respects. Dispersal typically refers to the movement of individuals in a population that results in an increase in the mean distance between individuals (Andrewartha & Birch 1954; Southwood 1981; Dingle 1996). According to Danthanarayana (1986) and Dingle (1996), migrants usually exhibit five basic behavioral characteristics: 1) persistent movement, 2) undistracted by the presence of resources promoting growth and maintenance (Kennedy 1961), 3) “straightened out” movement, 4) distinct leaving (Southwood 1962) and arriving behaviors, 5) reallocation of energy specifically to support movement.

In the United States *Aphonopelma* can be found west of the Mississippi River to the Pacific Coast and north into Arkansas, Utah, and Nevada (Baerg 1928; Gertsch 1979; Roth 1993). They are typically found on hillsides covered in sparse vegetation and mixed with diverse desert growth (Baerg 1928, 1958; Gertsch 1979). Tarantulas are usually nocturnal, but may be active from late afternoon into late morning when light levels are low (Baerg 1958; Comstock 1975; Minch 1978).

Radio telemetry is an effective tool for collecting data on organisms that are difficult to follow, observe or relocate (Mech 1983). His-

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torically, it has been used extensively to follow the movements of larger animals (Mech 1983). As technology decreased the size of transmitters, this technique has been increasingly applied to smaller invertebrates including crayfish (Covich 1977), crabs (Gherardi et al. 1987, 1988a, b, c; Gherardi & Vannini 1989; Fletcher et al. 1990), snails (Bailey 1989; Tomiyama & Nakane 1993), and insects (Hayashi & Nakane 1988, 1989; Riecken & Rath 1996). Radio telemetry may provide unique insights into the ecology and behavior of the larger arachnids. This technology is used to study the brown tarantula, *A. hentzi*, an ideal subject for radio telemetry due to its activity, abundance and size.

METHODS

Study site.—The study was conducted on the W.T. Waggoner Estate, 19.4 km WSW of Electra, Wilbarger County, Texas (33°58'N, 99°08'W). This area is part of the Rolling Plains region of Texas, which is a subsection of the Great Plains region of the central United States (Lewis 1962). It is characterized by rolling-to-rough topography broken by intermittent streams (Lewis 1962). Annual rainfall for the area is approximately 76.2 cm, with May and September being the wettest months (Lewis 1962). The dominant vegetation is scrub mesquite (*Prosopis*), goat bush (*Caste-la*), prickly pear cactus (*Opuntia*), turkey cactus (*Opuntia*), little blue stem (*Schizachyrium*), mesquite grass (*Bouteloua*), and broom weed (*Xanthocephalum*). The southern portion of the study site is dissected by a paved farm-to-market road running east to west. The area is broken by occasional dirt or gravel maintenance roads. Past and current land use at the site include oil production and cattle grazing.

Transmitters and receiver.—All radio telemetry equipment was purchased from Wildlife Materials, Inc. (Carbondale, Illinois). A model TRX-1000S receiver was used with a folding three-element yagi directional antenna. The frequency range used was 150.000–150.999 Mhz. Each transmitter (SOPB-2011) had a different frequency thereby identifying individuals. Transmitters weighed approximately 0.6–0.8 g and were $9 \times 5 \times 4$ mm. The flexible antenna, constructed of wire similar to guitar string, was 7.62 cm in length. To prevent possible chafing of the abdomen and

to provide minimal physical contact the antenna was bent upward at a 45° angle.

Procedure.—Male tarantulas were equipped with transmitters from 2 September–17 October 1994 and from 9–19 July 1995. They were captured in a clear plastic container on predominantly open ground. Individuals were examined to determine overall physical condition. Those lacking obvious physical abnormalities and exhibiting activity were weighed (to the nearest 0.1 g) using an Ohaus LS200 portable scale. The only exception was specimen #13-94, which was missing the third left leg. Males ranged from 2.5–7.5 g. They were anesthetized with carbon dioxide for 2 min or until docile. Tarantulas were then placed on a thick synthetic sponge with legs extended. Their legs were restrained by placing a second sponge which had been cut to expose the cephalothorax and abdomen over the first sponge. String was used to hold the two sponge pieces in place. This restrained the spider and facilitated attachment of the transmitter. To assist in the attachment of the contact adhesive, the “hairs” (setae) were removed from an area on the carapace, posterior to the eyes, by gently rubbing the area with a pair of forceps. A small amount of waterproof contact adhesive was placed on the the carapace and on the transmitter. After 5 min the adhesive on the transmitter was pressed into the adhesive on the spider. This was allowed to set for 20–40 min before the tarantula was removed from the sponge and placed back into the capture container. Equipped tarantulas (Fig. 1) were released at the exact site where they were collected within 2 h of capture.

Tarantulas monitored in the fall of 1994 were observed a minimum of three days per week, while those in 1995 were observed once everyday, weather permitting. Locations of spiders were marked and labeled using flagging tape on adjacent vegetation. Direction traveled since the last observation was determined by compass. Readings were corrected to reflect true north. Approximate distance traveled between observations was obtained using a tape measure or by pacing.

Seventeen *Aphonopelma hentzi* males were monitored in the Fall of 1994 for movement. Of these, seven individuals retained their transmitters for four or more days and were considered for data analysis. This yielded a total of 113 observations. Six additional males



Figure 1.—*Aphonopelma hentzi* male with attached radio transmitter.

were monitored in July 1995. These individuals were checked for short-term movement once every 24 hours. Four of these individuals retained their transmitters for three or more days, and yielded 20 observations.

Identification.—The tarantula population studied was identified as *Aphonopelma hentzi*. Representative specimens are on deposit in the American Museum of Natural History, New York. The study site lies outside the known distribution reported by Smith (1994) for three species in the region. As a result, a name could not be assigned to this spider using Smith's (1994) descriptions. The validity of Smith's species are in question (Prentice 1997). Cokendolpher (pers. comm.) noted that Smith failed to take individual variation into account. Therefore, the old name is applied to the common tarantula of Texas and Oklahoma. Representative specimens from the area were confirmed as *A. hentzi* by Dr. Rick West, Research Associate, Royal B.C. Museum (West pers. comm.).

Statistics.—The samples from each year were compared using the Mann Whitney *U*-test for unmatched pairs (Fowler & Cohen 1990). There was a difference between the

samples when weight was considered ($U = 0$, $P < 0.05$). However, there was no difference between the samples when the rate ($U = 10$, $P > 0.05$) and inflection points per day ($U = 14$, $P > 0.05$) were considered. Based upon these data, the samples from both years were combined for statistical analysis except where indicated.

RESULTS

Movement.—Figures 2–6 illustrate the movement of males and give a brief description of the habitat for each observation. The weight ($\bar{x} = 5.0 \pm 1.5$ g SE), total time observed, total path distance, rate ($\bar{x} = 53.8 \pm 25.7$ m/d SD), number of inflection (turning) points per day ($\bar{x} = 0.64 \pm 0.19$ SD), point-to-point distance (distance from the first observation to the last observation), and point-to-point angles with 0° being north (angle from first observation to last observation) ($\phi = 253.6^\circ \pm 70.8^\circ$ SD) for each male are presented in Table 1. Male #12-94 traveled the farthest with regard to both point-to-point distance and rate (Fig. 4, Table 1). The most inflection points per day was exhibited by #5-94 in 1994 (Fig. 6, Table 1) and #1-95 in 1995

Table 1.—Individual tarantula number, weight, days observed, total distance of path traveled, rate of travel per day, number of inflection points per day, distance from first observation to last observation, direction from first observation to last observation.

Spider #	Weight (g)	Total time observed (d:h:min)	Total path distance (m)	Rate (m/d)	Inflection points per day	Point-to-point distance (m)	Point-to-point angle (degrees)
1-94	—	4:18:35	148.8	31.2	0.60	102.1	236
5-94	7.0	24:00:00	1320.2	55.0	1.00	677.3	327
9-94	6.6	4:17:26	281.4	59.6	0.60	208.2	141
10-94	6.2	7:17:14	412.8	53.5	0.75	264.2	114
12-94	7.5	18:10:27	1750.2	94.9	0.72	1360.4	305
13-94	5.3	4:15:48	123.9	26.7	0.60	116.9	228
18-94	6.6	13:22:26	364.2	26.1	0.50	272.2	313
1-95	3.6	9:22:09	815.6	82.2	0.80	324.6	98
2-95	—	3:00:34	211.1	69.9	0.66	188.3	215
3-95	2.6	2:22:50	222.2	75.8	0.66	176.3	243
6-95	4.2	3:22:55	69.2	17.7	0.25	14.1	6

(Fig. 5, Table 1). Male #6-95 traveled the least with respect to rate, inflection points per day and point-to-point distance (Fig. 3, Table 1). There was no correlation between tarantula weight and rate ($r_s = 0.10$, $n = 9$, $P > 0.05$). However, there was a marginally significant correlation between rate and inflection points per day ($r_s = 0.68$, $n = 11$, $0.02 < P < 0.05$).

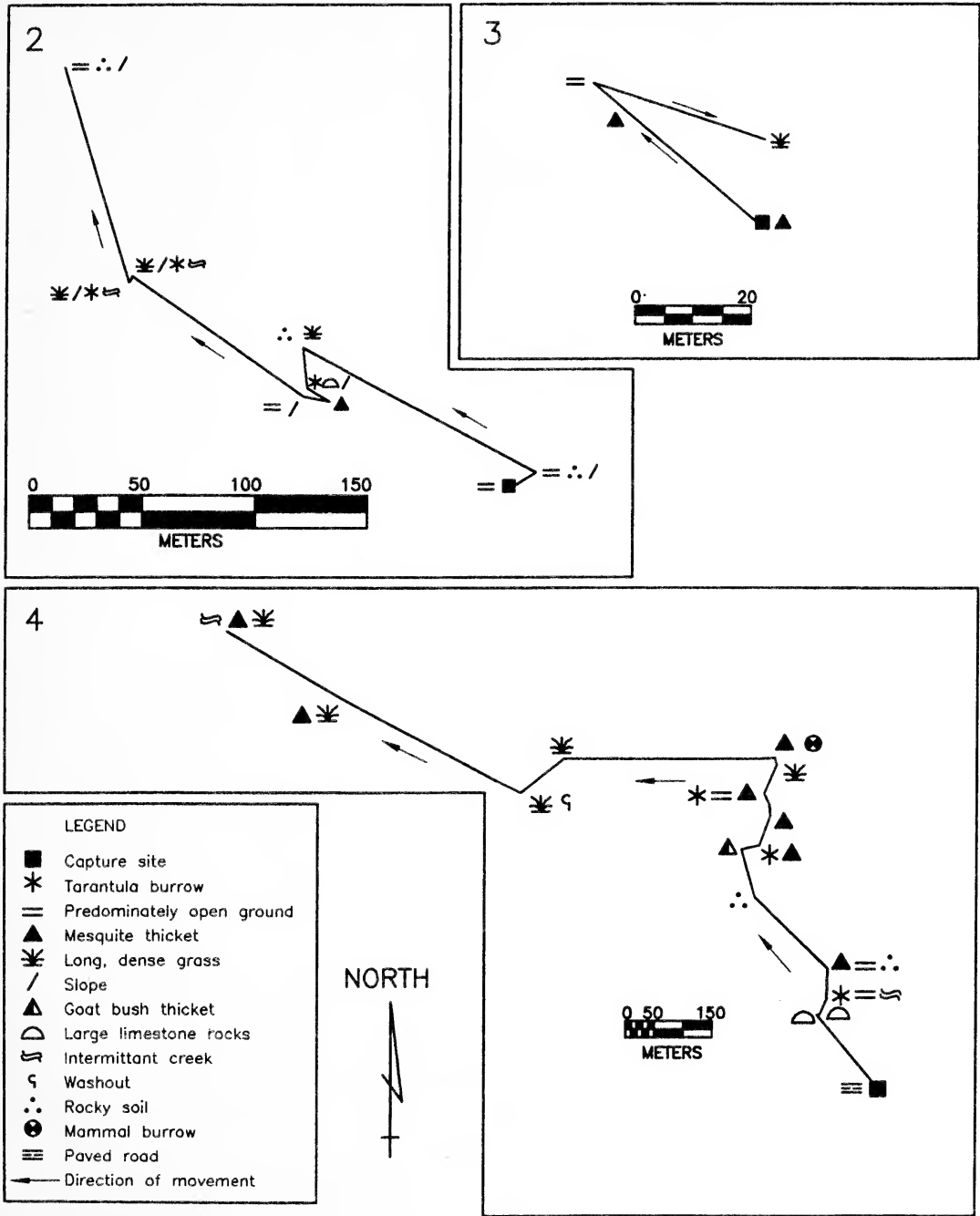
Overall movement of individual males was in almost all directions (Table 1). The Rayleigh test [uses the mean vector (r) to determine directedness (Batschelet 1981)] could not exclude randomness as a factor in the point-to-point movement of the combined samples from both years ($r = 0.23$, $n = 11$, $P = 0.5$) or of the sample from 1994 ($r = 0.31$, $n = 7$, $P = 0.55$). However, the movement of male #5-94 ($r = 0.46$, $n = 26$, $0.001 < P < 0.004$; $\bar{\phi} = 328.9^\circ \pm 59.7^\circ$ SD) and male #12-94 ($r = 0.62$, $n = 18$, $P < 0.001$; $\bar{\phi} = 335.4^\circ \pm 49.7^\circ$ SD) indicated directedness. The results from Rao's spacing test [uses angular data to determine directedness (Batschelet 1981)] yielded similar results with one exception; #13-94 exhibited directedness ($U = 188$, $n = 5$, $P < 0.05$; $\bar{\phi} = 247.1^\circ \pm 34.1^\circ$).

Performance of transmitters.—All transmitters, except one, were recovered in working order at the end of the study. The transmitter attached to #5-94 was recovered completely wrapped in silk within the entrance of a tarantula burrow. There were abrasions and breaches on the epoxy coating of the transmitter and a very large tarantula with

a taunt abdomen was observed within the burrow. There was no correlation between rate (m/d) and the percentage of the transmitter weight to body weight ($r_s = 0.104$, $n = 9$, $P > 0.05$). Three transmitters were known to have been removed from spiders within burrows. These transmitters were tightly wrapped in silk, and recovered just inside the burrow or a few centimeters from the burrow entrance.

Microhabitat and refugia.—Males were found moving through a variety of habitats from relatively barren, rocky ground to areas of dense vegetation. Tarantulas were observed to be traveling easily through the grass many centimeters above the ground. One male was observed hanging from vegetation several centimeters above the ground.

Most males were inactive during the day and remained in sheltered environments (e.g., scrub thickets). Scrub thickets were 1–3 m in height, 1–3 m in diameter and dominated by mesquite (*Prosopis*). Other plants included goat bush (*Castela*), prickly pear cacti (*Opuntia*), turkey cacti (*Opuntia*) and an understory of dense grasses (*Schizachyrium*, *Bouteloua*). Several small mammal burrows, outcroppings, and large limestone rocks were also used for shelter during the day. One locale, characterized by limestone slabs 0.5 m in diameter and interspersed in dense grass, attracted three males within two days yielding a total of five observations. The abundance of data obtained

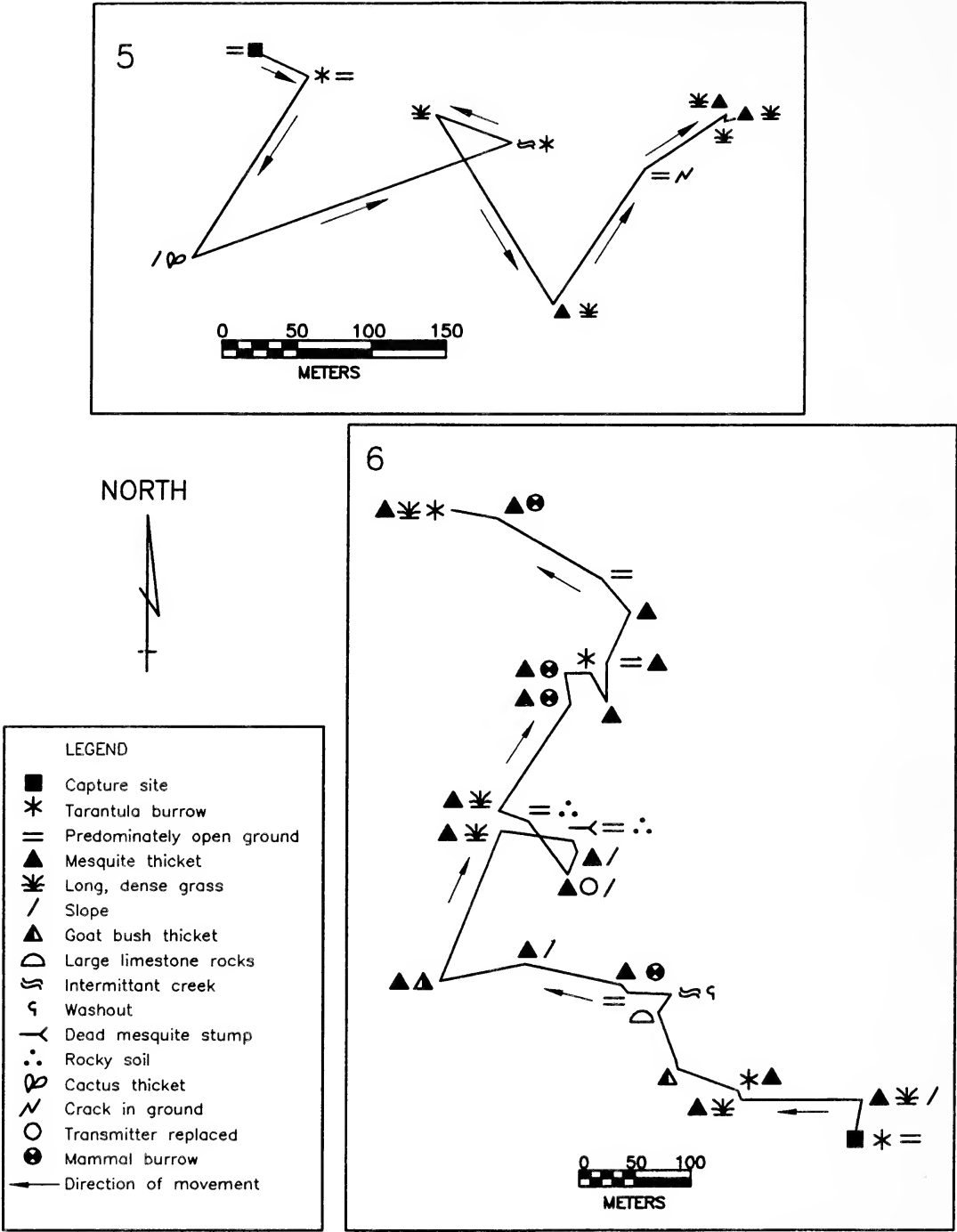


Figures 2–4.—Movement of *Aphonopelma hentzi* males. 2. Male #18-94 had the lowest rate and number of inflection points per day in 1994; 3. Male #6-95 had the lowest rate and number of inflection points per day in 1995; 4. Male #12-94 had the highest rate in 1994.

at this locale was not typical of data collected during the rest of this study.

Seven males were found within burrows with individuals that were assumed to be ma-

ture females. Males remained at these locales from 1–3 days before continuing movement. Female burrows were found by males within thickets, in dense grass and on open ground.



Figures 5, 6.—Movement of *Aphonopelma hentzi* males. 5. Male #1-95 had the highest rate and number of inflection points in 1995; 6. Male #5-95 had the highest number of inflection points per day in 1994.

Males probably visited more female burrows than detected due to the cover provided by dense vegetation. These "locales" or "sites" were not closely inspected for fear of disturbing the males and biasing movement results.

Behavioral observations.—On 2 September 1994 male #1-94 was observed mating with a female approximately 0.5 m from the entrance of the female's burrow on barren soil. Upon approach the spiders separated and then the female quickly retreated into her burrow. The male was captured and outfitted with a transmitter. Male #5-94 was 45.7 cm from her burrow for at least 18:54 h.

On two separate occasions males were observed moving in overlapping counter-clockwise circles 60–90 cm in diameter. This is similar to observations made by Shillington & Verrel (1997).

Observations towards the end of the summer indicated most males continually lost body mass and ultimately possessed very small abdomens. On the morning of 3 October 1994 male #12-94 (Fig. 4) was found in the open, positioned vertically with his abdomen in the air. The last two pairs of legs were stroking the antenna of the transmitter. His abdomen was very small. In the evening he was found dead, legs curled under the shrunken abdomen. Males #2-95 and #3-95 were also found dead. However, males #1-95 (Fig. 5) and 6-95 (Fig. 3) were recovered, transmitter removed, and released at the end of the 1995 study period.

DISCUSSION

The movement of male tarantulas has been a subject of speculation and interest to arachnologists for many years (Smith 1994). Most of what is known regarding the ecology of male tarantulas has been obtained from studies regarding the ecology of female and immature individuals within the proximity of their burrows (Minch 1978, 1979a, b, c; Kotzman 1990; Shillington & Verrell 1997) or in the laboratory (Baerg 1938, 1963), with two known exceptions (Baerg 1958; Sanderson 1988 as cited by Smith 1994). This is the first study known to extensively document the movement of male tarantulas.

Radio telemetry proved to be useful and enabled us to obtain data that would have been difficult to acquire using other methods. The

performance of the transmitters was excellent. The signal could be detected several hundred meters from the spider. In addition, the males could be located easily when in burrows and under rocks. It was assumed the transmitters would have a minimal effect upon the movement of individual tarantulas. Maneuverability in small spaces was a concern, but the antenna proved flexible enough to allow males to enter and remain in burrows. Tagged males were observed crawling around or past residing females within the burrow.

Attachment of the transmitter to the tarantula was a problem. Many of the contact adhesives used did not maintain their bond. This resulted in several spiders losing their transmitters within a few days and was the limiting factor of this study.

Organisms use a hierarchical set of cues to locate resources and exhibit behaviors appropriate for each level: habitat, patch, individual resource. (Bell 1991). It has been shown (Baerg 1958; Minch 1979c; Shillington & Verrell 1997) that male tarantulas are able to detect local "cues" provided by females in the vicinity of their burrows. These have not been shown to be directional, but do elicit local search behavior described as "animated circular motion" (Shillington & Verrell 1997), and were observed in this study. Baerg (1928, 1958), Gabel (1972), and Kotzman (1990) have noted the clumped or patchy distribution of theraphosid burrows. Theraphosids are almost blind and cannot see beyond 2.5–5 cm (Baerg 1958). As a result, it is unlikely tarantulas use visual environmental cues when searching for burrow patches. Bell (1991) proposed several search strategies organisms may adopt when lacking environmental cues while searching for resource patches: random walk, straight line, systematic movement pattern (spiral or parallel movement), kinesthetic-input mapping or a combination of these strategies. The results of this study did not reveal a systematic movement pattern, and this may be because observations were not at the appropriate scale. Three large scale loops were observed among individuals considered for data analysis (Figs. 5, 6). These imply male tarantulas are conducting systematic searches to locate mates within "colonies." The movement of searching males between "colonies" may be a combination of random walks and straight line movements as indicated by the

directedness expressed in only a few individuals. However, the lack of directedness may be a function of the time individuals were followed.

There was limited evidence to support the axiom that male tarantulas are migrating using Dingle (1996) and Danthanarayana's (1986) definition. Based upon their observations of North American tarantulas, Baerg (1963) and Minch (1978) report that males travel farther during the mating period than any other period of the life cycle. There was some evidence that movement of individuals was directed. Later in the season males were observed with notably smaller abdomens indicating energy may be reallocated specifically for movement. Male #12-94 (Fig. 4) moved 30% (537 m) of the total distance (1750 m) in 9% (1 day, 16h, 25 min) of the total time (18 days, 10h, 27 min). Baerg (1928) and Minch (1979c) noted that males die at the end of the mating season. Their observations noted that preceding death the abdomen becomes shrunken, ability to extend legs is lost, and overall sluggish behavior occurs. There was little evidence for a synchronized, directional movement of all males sampled. As a result, no definitive conclusions can be drawn regarding the characterization of the movement of male tarantulas as migratory. Further behavioral studies would serve to elucidate the characterization of this behavior.

Early summer males were smaller in size and weight. As a group they were not significantly different with respect to their rate and inflection points per day, and they behaved the same ecologically with regard to movement. Further study is needed to determine if the early males have overwintered as adults or simply molted earlier than the late summer brood.

Males frequented scrub thickets, small mammal burrows and large limestone rocks throughout the study. These habitats probably provided protection from predators and allowed better thermoregulation during the day. In addition, the locale characterized by limestone rocks may have a high density of mature females not observed due to burrows being hidden by the rocks.

Males were frequently found within tarantula burrows in the presence of other individuals. These were presumed to be mature fe-

males and males were courting and mating with them. Multiple matings with the same female are probable given the length of time males were in the presence of these females, which ranged from one to several days. Males also visited multiple females (Figs. 2, 4, 5, 6). The data reflect fewer matings than probably occurred due to sampling and lack of detection within thickets. Baerg (1958) suspected mating occurs primarily inside the burrow. However, male #1-94 was observed mating with a female approximately 0.5 m from her burrow entrance.

This study indicates radio telemetry is a valuable technique for studying the movement of male *Aphonopelma hentzi*. Males were observed moving large distances, up to 1300 m, over a significant period of time, up to 18 days, while searching for mates. Current research on the behavior and ecology of movement in tarantulas includes: evaluation of extensive movement, influence of different habitat types, effect of habitat fragmentation.

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PHENOLOGY AND LIFE HISTORY OF THE DESERT SPIDER, *DIGUETIA MOJAVEA* (ARANEAE, DIGUETIDAE)

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ABSTRACT. The desert spider, *Diguetia mojavea* Gertsch 1958, is a numerical dominant in many California deserts. We report data collected over a three-year period (1984–86) on reproduction, life history, phenology, microhabitat, prey, and dispersion for *D. mojavea* in the Coachella Valley, California. This is one of few studies to calculate life history table parameters for a desert arachnid. The average female laid 1065 eggs, while the net reproductive rate (R_0) was 1.41; generation time (T) was calculated as 204.85 days. These spiders appear to fit a Type III survivorship curve. Density of *D. mojavea* was typical for a desert spider at 0.02 spiders/m². Finally, our findings complement the only other study on *D. mojavea* (Nuessly & Goeden 1984).

Spiders in the family Diguettidae Gertsch 1949 are primitive, six-eyed weavers contained in three genera, *Pertica* Simon 1903, *Segestrioides* Keyserling 1883 and *Diguetia* Simon 1895 (Platnick 1989). *Diguetia*, the dominant genus in this family, consists of spiders with elongate legs that weave characteristic funnel or net webs, or a combination thereof. Although they range widely from the southwestern United States to southern Mexico (Comstock 1948; Gertsch 1958; Lopez 1984) and parts of Argentina (Gerschman de Pikelin & Schiapelli 1962), few papers have focused on this family since its formal description by Gertsch (1949). Gerschman de Pikelin & Schiapelli (1962) studied the web characteristics of *D. catamarquensis* (Mello-Leitão 1941) in Argentina, Eberhard (1967) investigated prey capture and wrapping behavior in *D. albolineata* Simon 1898, and Bentzien (1973) described behavior and reproductive biology of *D. imperiosa* Gertsch & Mulaik 1940. *Diguetia canities* McCook 1895, the most widespread species (Cazier & Mortenson 1962), is best-studied due both to its relative abundance and its commercial importance in insecticide development (e.g., Krapcho et al. 1995; Hughes et al. 1997).

Diguetia mojavea Gertsch 1958 is distributed throughout southern California and adjacent areas in Nevada (Gertsch 1958), and it also appears to be one of the numerically dominant spider species in some California desert areas (Polis 1991). However, only one paper (Nuessly & Goeden 1984) focuses on

the biology and ecology of this species, and a few others mention *D. mojavea* briefly (e.g., Polis & McCormick 1986; Polis 1991). Here, we examine *D. mojavea*'s phenology in more detail. We also report life history statistics used to calculate *D. mojavea*'s net reproductive rate and rate of potential increase both because of its significant role in various desert ecosystems and its potential impact as an important biological control agent (Nuessly & Goeden 1983).

METHODS

Relevant biology.—Several characteristics facilitate research on *D. mojavea*. First, populations are relatively dense (see Results). Second, the web of adults is large (mean length: 33.8 cm; mean width: 24.0 cm; see also Nuessly & Goeden 1984) and quite visible, especially in early morning or late afternoon at low sun angles. Third, the adult female web includes a retreat containing eggs, thus facilitating studies on reproductive biology. Fourth, prey and diet are easily quantified because *D. mojavea* incorporates most prey into its web (Gertsch 1958).

Study site.—Field studies were conducted within and adjacent to the Coachella Valley Reserve of southern California (Riverside County, California; 33°54'N, 116°37'W). The Reserve encompasses about 780 km² and spans an elevational gradient from 320 m in the northwest to sea level in the southeast. Winters are mild; summers, hot and dry. Air temperature in July annually exceeds 40 °C

and temperatures greater than 50 °C occur (Edney et al. 1974; Polis 1988). It is a low elevation rain shadow desert, with annual rainfall at the University of California's Deep Canyon Field Station averaging 116 mm, ranging from 34 mm in 1961 to 301 mm in 1976. Vegetation includes *Atriplex caescens* (saltbush), *Salsola australis* (Russian thistle), *Larrea tridentata* (creosote), *Tamarix* sp. (salt cedar), and annual plants and grasses. We surveyed web sites dispersed over an area of 7500 m² divided into 300 quadrats, each 5 × 5 m. Quadrats were marked with flags and surveyed at least every three weeks from early June to September in 1984–86. Webs and egg sacs were also collected in December 1984–86 and 1997.

Egg sac analysis.—*Diguetia mojavea*'s egg morphology and egg sac construction are similar to *D. canities* (Cazier & Mortenson 1962). Each sac is constructed beneath the previous one in a shingle-like fashion, which is then incorporated into the tube retreat (Gertsch 1979). To examine seasonal patterns in egg-laying in August, September, and December 1984–86, we randomly chose 31 retreats to examine the number of egg sacs. All females were usually absent in our December survey (see Life history results); thus no new egg sacs could be laid, and these data are then used to estimate average number of egg sacs laid in a female's life. Egg sacs were dissected for egg counts. Stages within the sac were classified as either egg, embryo/deutovum, 1st instar, 2nd instar (based on cephalothorax length), or dead. Because maternal-guarding of the egg sacs seemed to play an important role in the life history of the adult females, we assumed each web contained only the resident female's eggs. Here as throughout the paper, means are reported with their standard deviations.

Spider web/microhabitat analysis.—For each spider in our quadrats, we recorded life stage (spiderling, adult) and sex of adults. Web characteristics were collected for the 137 webs in our plot in 1984. The volume of each web was calculated using height, width, and length. We measured retreat height and identified the plant on which webs were placed. Entire retreats and egg sacs were randomly collected in 1985–86 outside our quadrats. These were preserved in alcohol. For these spiders, we recorded adult-spider mass, the

number of egg sacs and the egg stage (see above) for each web.

Prey analysis.—We examined diet by analyzing the prey from 111 retreats collected from 1984–86. Most prey are incorporated into the web, but some very large prey were discarded into the sheet or onto the ground. Prey items were easily separated from the web using a dilute bleach solution (Nuessly & Goeden 1984). A separate sub-sample ($n = 26$) of prey was taken from the sheet-web for analysis. Collected prey were identified to order and/or family.

Dispersion, phenology and life history.—The 300 quadrats in our survey area of 7500 m² were censused throughout the study to determine *D. mojavea*'s density, phenology and dispersion. These data were used to calculate survivorship curves and a Greig-Smith block size analysis in 1984 (Pielou 1977). This particular dispersion analysis determines if organism-spacing is aggregated, regular, or random. Fecundity variables (Pianka 1978) were also calculated. Parameters l_x (fraction of surviving spiders at age X) and m_x (number of offspring produced by an average spider at age X) were used to calculate net reproductive rate (R_0) and generation time (T). All formulae follow Pianka (1978).

RESULTS

Phenology.—The life cycle of *D. mojavea* encompasses approximately one year. Spiderlings emerge in late December through March. Females mature in May through June; the first egg sacs are produced in August through September (Figs. 1, 2), 2–3 months after the last molt. Approximately 85% of all egg sacs are laid during this two month period. Adult males first appeared in July. From 1984–86, adult females senesced and died from October to mid-December. In 1997, a few adult females were observed living in their webs as late as 20 December (7 out of 31). Males typically died one to two months before females (Fig. 2). We observed males in 14% of the 137 webs collected in July–September. The average mass of the adult females was 36.8 ± 23.6 mg, with a mean carapace length of 3.8 ± 0.8 mm. From our 1997 sample, the mean carapace length of 1st instar spiderlings was 0.66 ± 0.03 mm.

Egg sac analysis.—All egg cases appeared to be laid by late September. One to 13 total

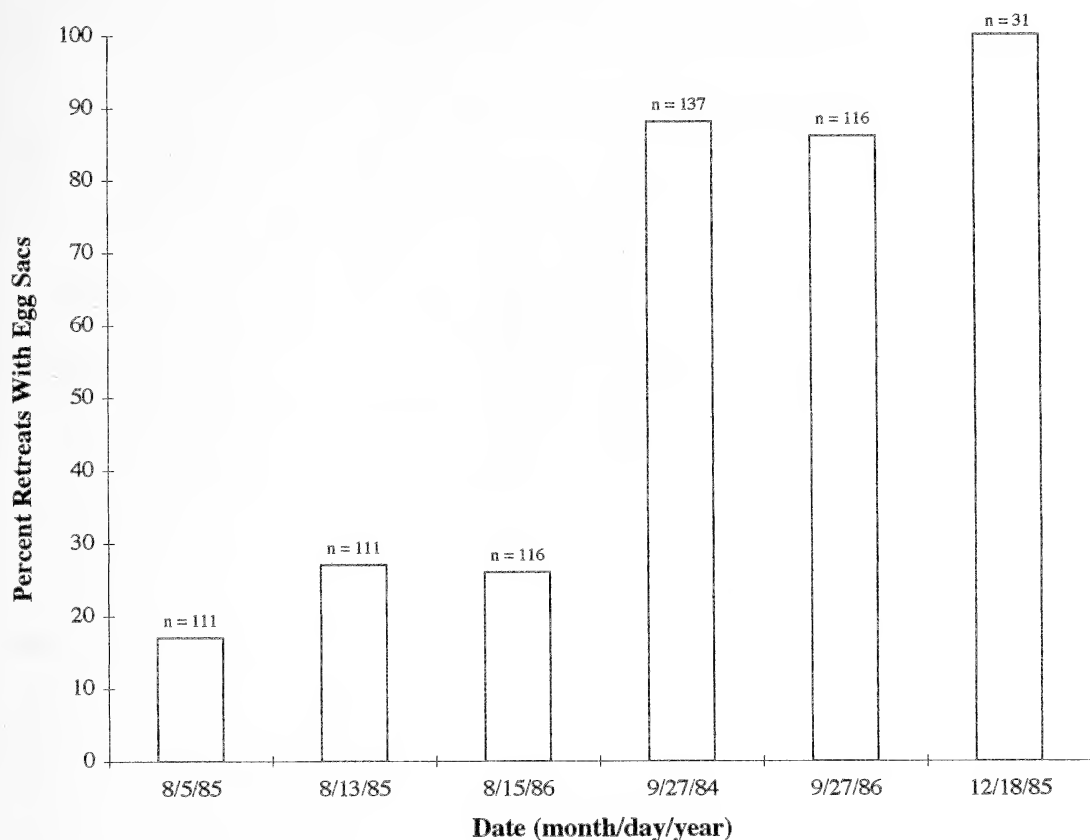


Figure 1.—Oviposition phenology. Seasonal changes in percentage of webs of *D. mojavea* found with egg sacs ($n = 96$).

egg cases were laid per female. All 31 retreats examined in our December collection contained egg sacs (Fig. 1); the number of egg sacs and the total number of eggs a female laid were significantly correlated (Fig. 3). Over the three-year period (1984–86), we collected 364 webs that contained 1083 intact egg cases. The average number of egg cases per female was 4.9 ± 2.7 (Fig. 4). The mean number of eggs per sac from 1984–86 was 217.4 ± 31.6 , data taken from a subsample of 237 egg cases. Thus, the mean number of eggs laid per female was 1065.3 ± 381.2 .

Egg sacs were laid over a period of days as evidenced by personal observation, presence of multiple egg sacs, and staggered emergence of spiderlings. We examined the stage of development for the dissected sub-set ($n = 237$) of the egg sacs we collected. Each case contained only individuals in the same developmental phase. However, developmental stage did differ among egg cases within a particular

female's retreat. Of the 237 cases examined, 47% ($n = 111$) were classified as containing eggs; 19%, embryos (deutova); 17%, 1st instar; 4%, 2nd instar; and 13%, shriveled, dead eggs. The sequence of development followed the order in which the sacs were deposited: the uppermost egg sac located at the tip of the retreat always contained the most advanced stage, and sacs toward the retreat opening contained only eggs.

Web/microhabitat analysis.—The first typical webs we noted were built in late May by spiders with a body length of 3–4 mm. As the summer progressed, webs became larger and were placed in progressively higher vegetation. The mean size of a web in early summer (10 June) was 28.3 cm in length (range: 10–50 cm) by 21.1 cm across (range: 10–43 cm). By mid-summer, mean size increased to 33.8 cm (20–60 cm) by 24.0 cm (12–40 cm). There was a significant correlation between spider weight and web volume (Fig. 5) and

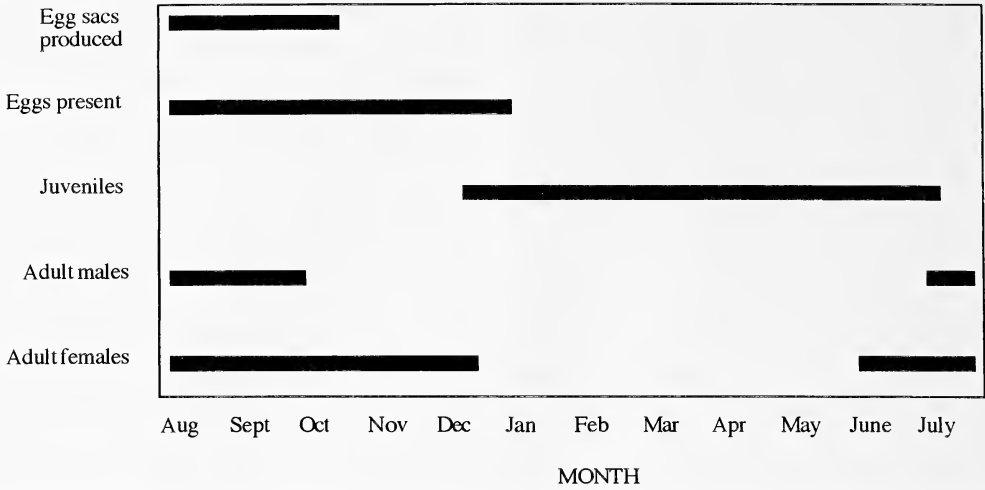


Figure 2.—Phenology. Bars show months in which each stage occurred. Data collected from 1984–1986.

between shrub height and spider weight (Fig. 6) (analyses conducted on July/August data).

Web location changed throughout the year with less desirable sites (i.e., dead bushes) supporting progressively fewer spiders. In early summer, 68.6% of the webs were built in perennial bushes (39.8% in *Atriplex* and 28.8% in *Salsola*), while the remaining 31.4% were placed in both living and dead annuals. *Larrea* and *Tamarix* were only rarely used as web-sites possibly due to their thin, exposed and flexible branches. Webs persisting into

late summer remained only on larger *Atriplex* and *Salsola* as winds damaged and uprooted annual plants. Moreover, 43.8% of monitored webs were torn by wind and/or abandoned; unprotected web sites near the ground represented 72.1% of these cases.

Prey analysis.—From May through October, spiders were observed feeding primarily in early morning or late afternoon, thus avoiding the mid-day heat. Prey capture was observed on several occasions. After prey were detected in the web, the resident would run to the prey and immediately (< 10 seconds) immobilize it with a bite. Silk, although used to secure prey to the web, was not used for immobilization (see also Eberhard 1967).

Prey remains were analyzed from 111 webs; a total of 6771 individual prey was identified to order and/or family (Table 1). On average, each web contained 61 ± 17.8 prey items; mean prey-size in retreats was 5.2 ± 0.9 mm. Homoptera (Cicadellids), small Hymenoptera, and Coleoptera comprised 88.1% of *D. mojavea*'s diet. A coleopteran egg predator (Cleridae, *Phyllobaenus discoideus*) was occasionally caught. Five other spider species comprised 3.4% of the diet and occurred in 30% of examined retreats. Cannibalism was recorded three times.

The sheet-web subsample ($n = 26$) yielded fewer (< 5 prey/sheet-web) but much larger prey (14.9 ± 6.0 mm; 131 prey analyzed). Only 3% of all prey items (mean = 1.9 ± 0.7)

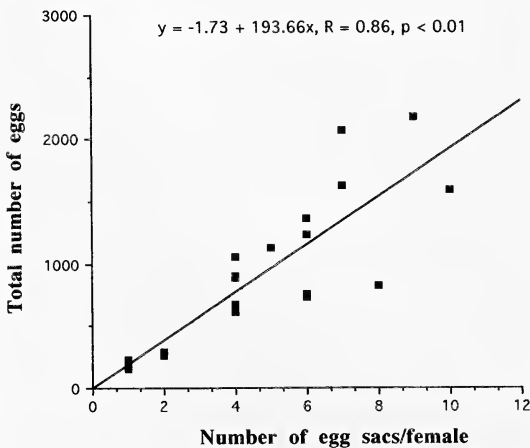


Figure 3.—Egg production. The number of eggs laid per female was significantly correlated with the total number of egg sacs ($y = -1.73 + 193.66x$, $R = 0.86$, $P < 0.01$), number of retreats examined = 31.

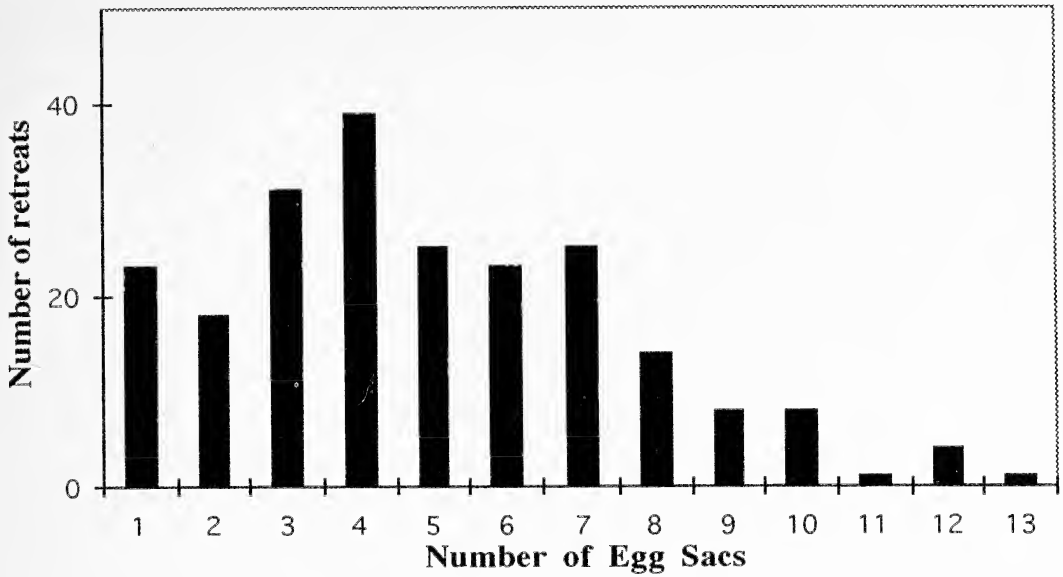


Figure 4.—Distribution of egg sacs in retreats. Egg sac number per retreat for data from 1984–1986 (total number of egg sacs examined = 364).

were dropped on the sheet-web by the spider. Although we did not measure biomass, large prey certainly represented more than 3% of total prey biomass. The largest prey items were a mantid (25 mm), mud dauber wasp (25 mm), robber fly (24 mm), and cicadid (24 mm). Grasshoppers were the most common

larger prey in sheet-webs but constituted less than 1% of *D. mojavea*'s total diet.

Mortality and survivorship.—Several predators were observed in diguetid webs. Clerid beetle larvae (*P. discoideus*), reported egg predators (Cazier & Mortenson 1962), emerged in the lab from about one-seventh of the webs analyzed ($n = 137$). Salticids were observed eating both diguetid eggs and adults;

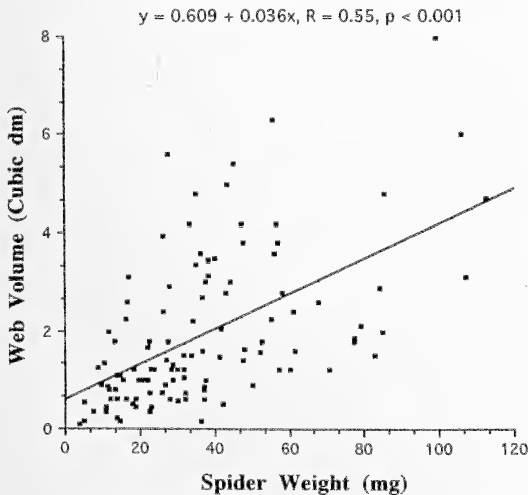


Figure 5.—Web volume as a function of spider mass. Spider weight was significantly correlated with web volume ($y = 0.609 + 0.036x, R = 0.55, P < 0.001$) for all three years combined (1984–1986).

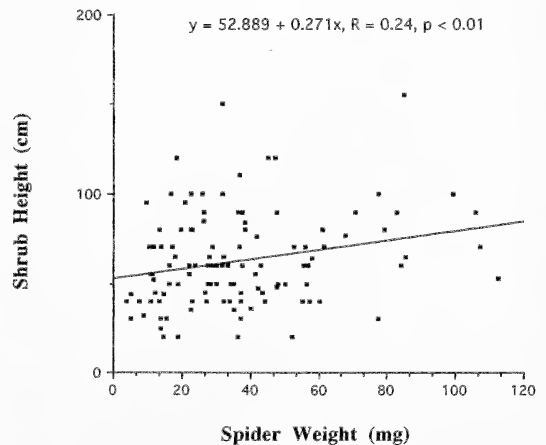


Figure 6.—Shrub height as a function of spider mass. Spider weight was significantly correlated with shrub height ($y = 52.889 + 0.271x, R = 0.24, P < 0.01$). Data are for all three years combined (1984–1986).

Table 1.—Prey of *Dignetia mojavica*. Italics indicate prey orders with families listed beneath when possible. Numbers in parentheses indicate total for the group.

Taxa	% of diet	% Occurrence among retreats
<i>Arachnida</i>	(3.4)	30
Diguetidae	1.0	
Mimetidae	0.8	
Oxyptidae	0.2	
Salticidae	1.4	
<i>Hemiptera</i>		
(e.g., Pentatomidae)	(2.2)	16.2
<i>Homoptera</i>	(36.7)	
Cicadellidae	33.9	80.2
Cicadidae	0.1	
<i>Isoptera</i>	(<0.01)	0.05
<i>Orthoptera</i>		
(e.g., Acrididae, Mantidae)	(0.5)	4.5
<i>Coleoptera</i>	(17.9)	61.3
Tenebrionidae	16.9	
Cleridae	0.01	
<i>Diptera</i>		
(e.g., Asilidae)	(3.4)	23.4
<i>Hymenoptera</i>	(33.5)	
Pompilidae	27.3	
Apidae	3.2	
Formicidae	2.9	
Sphecidae	0.1	79.3
<i>Lepidoptera</i>		
(e.g., Coleophoridae)	(2.2)	14.4

Habronattus tranquillus and *Metaphidippus manni* (G. & E. Peckham) appeared to be the most frequent predators of *D. mojavica*. Parasitism was not observed in this study.

Figure 7 shows average spider density through time summed over all quadrats in 1984. Adult density decreased in an almost linear fashion throughout the summer from July through September 1984, while egg production increased throughout each summer. If we assume that egg production in 1983 was similar in our plot to that in 1984, only 137 females in 7500 m² out of approximately 123,600 eggs survived to adulthood (< 0.01%). This represents a Type III survivorship curve (Pianka 1978). Finally, adult density decreased from 0.02 spiders/m² (137 spiders/7500 m²) in July to 0.003 spiders/m² (19 spiders/m²) in September.

Dispersion.—A Greig-Smith block size analysis of dispersion (Fig. 8) indicated that

these spiders were not randomly dispersed in our study plots. Significant aggregations appeared at block sizes of 1 and 8 m.

Life history.—We calculated life history statistics using the data on number of eggs laid per female and spiderling/adult emergence/survival. Table 2 summarizes fecundity variables (Pianka 1978). The empirical net reproductive rate, R_0 , (Pianka 1978) was 1.41, which was easily calculated since all spiders remaining at the end of the season were female. Generation time (T) was calculated as 204.85 days. The average number of eggs laid per female (1065.3) was applied to all adult females with egg cases, making m_x (the number of offspring produced by an average organism at age X) equal to 1.0 (or 100%) for August and September age values (i.e., egg cases were present in August through October; Fig. 2). For the July age class, m_x was 0.0 because no egg cases were observed before

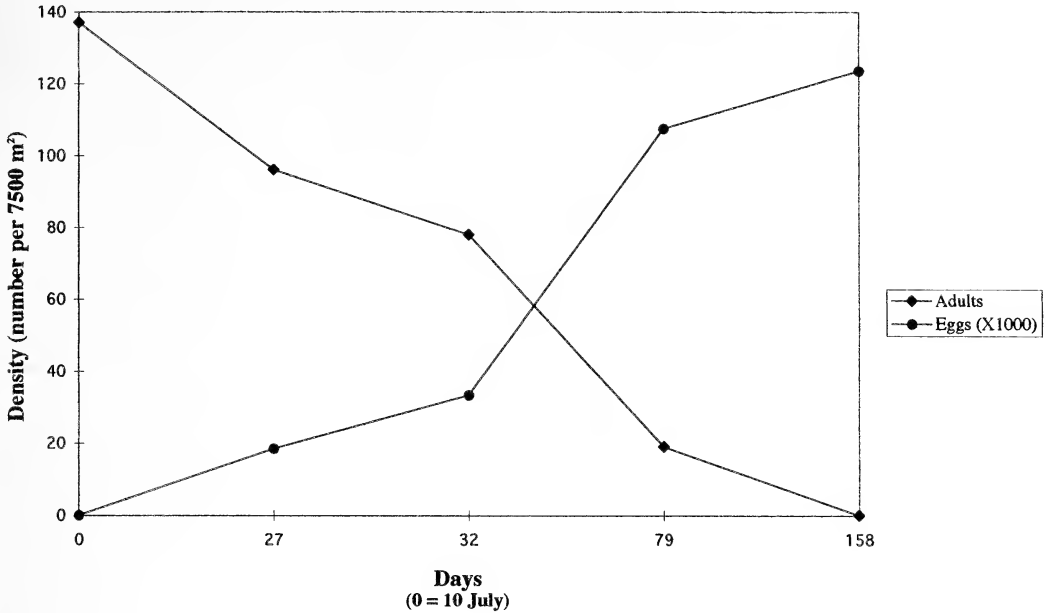


Figure 7.—Survivorship. Spider density decreases as time of season increases while egg number ($\times 1000$) increases throughout the season. Data are from 1984.

August. The maximum rate of natural increase, r_{max} ($\ln R_0/T$) was calculated as $1.68 \times 10^{-3}/d$.

DISCUSSION

There are a number of unique morphological and ecological characteristics exhibited by *D. mojavea*.

Phenology.—Recall that we observed

hatching of spiderlings in the field from December-March, adult females from June-December, adult males from July-October, and egg-laying from August-October. The univoltine and semelparous qualities of *D. mojavea* are typical of other diguetids (e.g., Bentzien 1973) and other spiders, in general (Foelix 1996). Moreover, a similar 1-year, 1-egg sac pattern is found in many desert arthropods, which may be due to the costliness of egg production and longevity in desert ecosystems (Polis 1991).

Reproduction and life history.—Our observations indicated that egg production in *D. mojavea* is slightly lower than that reported by Nuessly & Goeden (1984) (an average of 6.4 egg sacs/nest with a mean of 176 eggs/sac for a total of 1126 eggs/web). *Digueta mojavea*'s egg production fits well within the range of eggs produced by other spiders (Foelix 1996).

Staggered emergence is seen in spiders that have multiple egg sacs. This tactic may provide insurance against synchronous emergence during unfavorable conditions in harsh environments such as the desert. Thus, *D. mojavea* lessens the risk of failure through variable hatching times. Such a strategy is also seen in certain annual weed species and var-

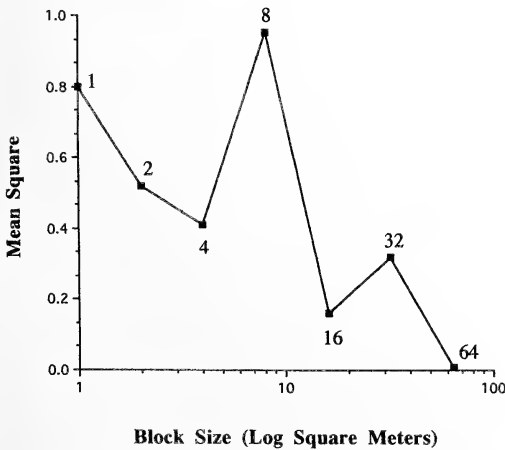


Figure 8.—Dispersion analysis. Greig-Smith block size analysis shows statistically significant aggregations at 1 and 8 m blocks. Data are from 1984.

Table 2.—Life history parameters calculated from the data collected throughout the study: l_x = fraction of spiders surviving at age X ; m_x = the number of offspring produced by an average spider at age X ; $l_x m_x$ = fecundity schedule; R_o = net reproductive rate; T = generation time (days). Formulae are based on Pianka (1978).

Age (X) in days	l_x	m_x	$l_x m_x$	$Xl_x m_x$
101	1.0	0.0	0.0	0.0
138	0.7	1.0	0.7	96.6
143	0.57	1.0	0.57	81.51
191	0.14	1.0	0.14	26.74
Total			$R_o = 1.41$	$T = 204.85$

ious other opportunistic species in the desert environment (Polis 1991). Staggered emergence is observed in most spiders that have multiple egg sacs (e.g., Bristowe 1958; Jackson 1978); it is probably an adaptation to high parasitoid pressure and/or harsh abiotic conditions.

The net reproductive rate indicates that this population could potentially increase 1.41 times per generation. The maximum rate of increase is one of the lowest ever reported (e.g., Pianka 1970) even when compared to other arachnids (e.g., scorpions from Polis & Farley 1980). This finding may reflect the high rate of egg mortality and low survivorship of females to first age of reproduction.

Mortality.—Our sample produced a Type III survivorship curve. Many desert inhabitants have high mortality rates in the early stages of their life history (Polis & Yamashita 1991), which may be caused by a variety of desert stresses. We observed a number of predators preying on diguetid adults and eggs. Nuessly & Goeden (1984), on the other hand, observed molting only as a cause of mortality in the field.

Prey analysis.—Spiders, on the whole, are usually characterized as generalist predators (Foelix 1996). Our results reinforce this generalization. *Diguetia mojavea* consumed prey from 10 orders. Homoptera, Hymenoptera, and Coleoptera made up most (more than 88.7%) of *D. mojavea*'s diet. This finding contrasts Nuessly & Goeden's (1984) report, who noted that the introduced biological control agent, a coleophorid moth, accounted for nearly 70% of *D. mojavea*'s diet in Indio, California; less than 3% of the diet in our study consisted of this moth. This discrepancy is probably due to the fact that Indio has had

several introductions of this moth for control of *Salsola*. Our site remains relatively undisturbed from this introduction.

Our analysis of prey contents in their sheet-webs is a first for diguetids. These prey had more biomass than those prey incorporated into the retreat but constituted a numerically minute (3%) amount of the total diet. This may be due to the inherent difficulty of capturing and/or handling larger prey.

Previous findings.—Nuessly & Goeden's (1984) paper is the only other study to examine the natural history of *D. mojavea*. They noted the following characteristics: a one-year life cycle; a diet consisting largely of coleophorids and cicadellids; a significant positive correlation between number of prey and egg number; and observed mortality due only to molting with no direct evidence of predation. They did not calculate life history parameters of reproduction and survivorship. Several differences existed between our study and that of Nuessly & Goeden's (1984). Their study was conducted at Indio, California for six months, a recently cultivated area populated by an invasive weed community. Our study was much longer (3.5 years) and was conducted on the floor of the Coachella Valley, which is a natural, undisturbed area.

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HOST SPECIFICITY AND DISTRIBUTION OF THE KLEPTOBIOTIC SPIDER *ARGYRODES ANTIPODIANUS* (ARANEAE, THERIDIIDAE) ON ORB WEBS IN QUEENSLAND, AUSTRALIA

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ABSTRACT. We investigated host specificity, the effects of host size, and the effects of the size, structure and occupancy of host webs on the abundance of the kleptobiotic spider *Argyroides antipodianus* O.P.-Cambridge 1880. The kleptobiont is not host specific, but does prefer orb webs that are surrounded by a scaffold of threads (barrier-web). Across all hosts, host size had little effect on the abundance of the kleptobiont, while host density and the presence of other species of *Argyroides* on webs had no effect. Web diameter, although not strongly related to the abundance of *A. antipodianus* in the field, limited kleptobiont numbers in greenhouse experiments. On webs of the Golden Orb Spider, *Nephila plumipes* (Latreille 1804), numbers of *A. antipodianus* were not affected by size of the scaffold or by aggregation of host webs. However, presence of host males was associated with a significantly higher abundance of *A. antipodianus*, suggesting that these kleptoparasites may take advantage of distracted females and impose a cost on mating in *N. plumipes*.

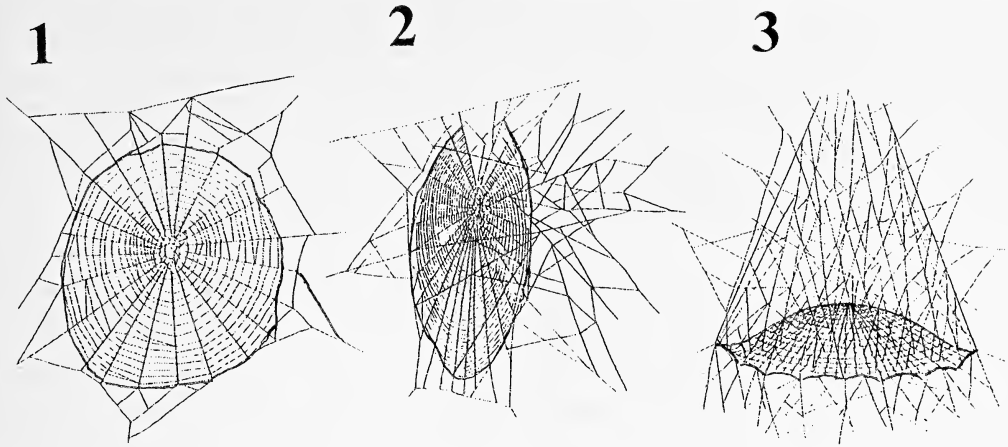
Many spiders of the genus *Argyroides* Simon 1864 live in close association with web-building spiders, and remove and feed on prey items captured in the webs of their hosts. These small web visitors are referred to as "kleptoparasites" or "kleptobionts" (Vollrath 1984, 1987; Elgar 1993). Although observations of their unusual foraging behavior are relatively common, little is known of the mechanisms that influence the infestation levels of kleptobiotic *Argyroides* on host webs. Abundance and diversity of *Argyroides* on webs may vary considerably among and within host species (Kaston 1965; Levi 1978, 1985; Whitehouse 1988; Elgar 1989), with up to 46 individuals and up to 3 species found on a single web (Exline & Levi 1962; Vollrath 1981).

The abundance of these kleptobionts may be influenced by a range of factors such as prey availability, weather, host behavior or web characteristics (Robinson & Robinson 1973; Smith-Trail 1981; Vollrath 1984; Larcher & Wise 1985; Vollrath 1987; Whitehouse 1988; Elgar 1989; Cangialosi 1990a, b; Whitehouse & Jackson 1993; Elgar 1993). Influential web characteristics could include size, architecture (e.g., relative size of web scaffold), abundance or aggregation of host

webs (Whitehouse 1988; Elgar 1993). Interactions with the host or other web "visitors," such as host males or other kleptobionts also could influence web colonization (Vollrath 1984, 1987; Grostal & Walter 1997).

Argyroides antipodianus O.P.-Cambridge 1880 is an abundant kleptobiont on the webs of orb weaving spiders in southeast Queensland. This spider is a relatively small-bodied species (ca. 3 mm long), that is easily recognized in Australia by its conical, bright silver abdomen (Grostal, in press). *Argyroides antipodianus* is associated with at least ten host species that build four different types of web (orb, funnel, tangle and space), but in New Zealand the kleptobiont is most common on the non-cribellate, sticky orb webs of *Eriophora pustulosa* (Walckenaer 1841) (Whitehouse 1988; Elgar 1993). Consequently, Whitehouse (1988) refers to *A. antipodianus* as a host specialist (*sensu* Vollrath 1984).

In this paper we used field surveys to examine the host range of *A. antipodianus*, and to investigate how the abundance of this spider is influenced by the architecture, size and relative abundance of host webs, and presence of other species of *Argyroides* on these webs. We then examined *A. antipodianus* on webs of one of its common hosts, the Golden Orb



Figures 1–3.—Three types of orb web sampled during four surveys in eastern Queensland: 1. Orb only (e.g., *Eriophora transmarina*), frontal aspect; 2. Orb and barrier (e.g., *Nephila plumipes*), fronto-lateral aspect; 3. Orb and tangle (e.g., *Cyrtophora moluccensis*), lateral aspect.

Spider, *Nephila plumipes* (Latreille 1804) and determined the influence of the relative size of barrier-web, web aggregation and the number of host males on kleptobiont numbers. Finally, we used greenhouse experiments to establish the effect of orb size of *N. plumipes* on the retention of *A. antipodanus* on webs. We predicted that the kleptobionts would be positively associated with web size and web aggregation, but negatively associated with numbers of other kleptobionts and of host males.

METHODS

Host range and abundance of *A. antipodanus*.—We conducted four surveys during 1995 in eastern Queensland: two surveys in the south east (Pinkenba 27°25'S, 153°07'E and Everton Park, Brisbane, 27°25'S, 152°59'E), one on the central coast (Yeppoon, 23°07'S, 150°44'E) and one in the far north (Cairns 16°53'S, 145°45'E). The Everton Park site (area = 2500 m²) was surveyed during October and was dominated by a semi-closed dry sclerophyll forest. Pinkenba (area = 16,000 m²), surveyed in August, consisted of an open stand of casuarina. The site at Yeppoon (area = 12,000 m²) was censused in May and consisted of an open palm forest, while the one in Cairns (area = 3,920 m²) was a closed rainforest thicket, and was examined in August. The month and location of the surveys depended on the opportunity to visit the sites.

We searched each site for orb webs that were located up to 200 cm above ground level and were over 9 cm in diameter. Spiders that constructed smaller webs were often juvenile and thus difficult to identify. For each web we collected the following data: species of the web builder, the spider's body length (cephalothorax and abdomen, measured with a clear ruler to nearest mm), the diameter of the orb (to nearest cm), and the number and species of *Argyrodes* on the web. The webs were divided into three categories based on their architecture: orb only, orb with barrier, and orb with tangle (Fig. 1). A barrier is a three-dimensional scaffold of non-sticky threads in front of and behind an orb (Fig. 2). A tangle consisted of a dense tent-like scaffold (Fig. 3) that extended above and below the orb. Tangles were more complex and larger relative to orb size, than barriers. All *Argyrodes* species were collected and preserved in 80% ethanol for later identification. A sample collection of the spiders was deposited with the Queensland Museum (Brisbane, Australia).

Abundance of *A. antipodanus* on webs of *N. plumipes*.—We conducted two additional surveys on separate plots at Pinkenba (one during April, the other during May 1995). In the first survey we sampled the webs of adult *N. plumipes* only, and in the second survey we examined webs of all stages of *N. plumipes*. The plots were adjacent to the one previously sampled for a range of different hosts

(see above) and consisted of an open stand of casuarina. For both surveys, we searched each site for webs of *N. plumipes* up to a height of 2.5 m, using a stepladder for webs above 2 m. All data were collected as in the previous surveys, except that we used carapace width to measure host size (a more precise measure at the intraspecific level; Higgins & Rankin 1996).

Additionally, we recorded the presence of visiting host males on webs and we qualitatively assigned the webs into five categories, based the complexity of the barrier (0 = no barrier; 4 = most complex barrier). We categorized barrier complexity by visually comparing the size of the orb relative to the volume occupied by the barrier threads and their density (no. of threads/volume). To check the accuracy of this estimation, we collected 10 clean webs for each of the categories 1 to 4 (webs with barriers present). We used dissecting scissors to separate orbs from barriers during collection. Then, for each web, we cleaned the silk from any debris and separately weighed orbs and barriers with an electronic balance in the laboratory. We used these results to calculate the mean ratio (\pm SE) of barrier weight : orb weight for each category and to check if the categories are discrete (i.e., if the means significantly differ).

Finally, for the survey of adult *N. plumipes* we recorded whether host webs were aggregated or not. A web was ranked as aggregated if its threads overlapped or interlocked with those of another web (Elgar 1989). Aggregations containing webs of immature hosts were excluded from the sample.

Retention of *A. antipodanus* on webs of *N. plumipes*.—The experiments were conducted in a ventilated greenhouse (Brisbane, September 1995). We used female *N. plumipes* of two age groups: juveniles (10–11 mm long) and adults (27–32 mm long), but only adult females of *A. antipodanus*. The spiders were housed in large cages (170 × 170 × 170 cm) which were covered with a fine plastic mesh. Four wooden racks, composed of a central rod (165 cm high) with four arms, were placed in the corners of each cage to provide support for webs spun by host spiders (Grostal & Walter 1997). Eight cages were used for each experiment, which was repeated six times over 18 days. One *N. plumipes* was

placed in each cage 48 hours before each trial and allowed to spin a web.

Four adult and four juvenile *N. plumipes* were used for each experiment. First, we randomly removed four hosts (two juveniles and two adults) from their webs. Care was taken not to damage the web while removing the spiders. Thus, each test consisted of four webs of adult *N. plumipes*: two with hosts included and two with hosts removed, and four webs of juveniles: two with hosts present, and two with hosts removed. Ten *A. antipodanus* were then placed on each web. After 24 h we recorded the number of *A. antipodanus* that remained on the webs.

Statistical analysis.—For surveys of host range and abundance of *A. antipodanus*, we used linear regression to estimate the relationship of the number of *A. antipodanus* per web with: 1) host body length; and 2) diameter of host web. The effect of presence of other *Argyrodus* species (+/–) on webs on the mean number of *A. antipodanus* per web was analyzed using single-factor ANOVA. Prior to the analysis, data were log-transformed for normality. Data from all four sites were pooled for the above analyses. Finally, we calculated the mean number of *A. antipodanus* per web for each host species, on every site ($n = 27$). Then, we regressed these means against the density of the corresponding host species at a given site (no. individuals/10,000 m², see Table 1). We examined all regression data with scatterplots to check for non-linear relationships.

For surveys of *N. plumipes*, we regressed the number of *A. antipodanus* per web against width of host carapace and diameter of host web. The effects of: 1) aggregation of host webs (+/–); 2) presence of male *N. plumipes* (+/–); and 3) the rank of web barrier (0, 1, 2, 3, 4) on the abundance of *A. antipodanus* (number per web) were analyzed separately with single-factor ANOVA. For the greenhouse experiments, we compared the numbers of *A. antipodanus* retained on webs that were spun by juvenile and adult *N. plumipes*, with and without the hosts, using a two-way ANOVA. All data were normalized by log-transformation before analysis.

RESULTS

Host range and abundance of *A. antipodanus*.—A total of 744 webs was examined

Table 1.—Average body length (mm) of host spiders (cephalothorax + abdomen), density (no./10,000 m²) of host webs sampled and the average number of *Argyrodes antipodius* on three types of host web (orb only, orb and barrier, orb and tangle) at four sites in coastal Queensland: Everton Park, Pinkenba (both in south-east), Yeppoon (central-east) and Cairns (far north). Values are totals or means \pm standard errors.

Site/Web type/Host	Host length (No. webs/10,000 m ²)	<i>A. antipodius</i> per web
Everton Park		
Orb only		
<i>Araneus dimidiatus</i>	7.7 \pm 1.0 (156)	0.2 \pm 0.1
<i>Argiope</i> sp.	6.9 \pm 2.3 (16)	0
<i>Eriophora transmarina</i>	12.7 \pm 2.1 (24)	0.3 \pm 0.2
<i>Leucauge</i> sp.	6.7 \pm 1.4 (36)	0
Orb & Barrier		
<i>Nephila plumipes</i>	12.9 \pm 4.1 (292)	2.7 \pm 0.3
Orb & Tangle		
<i>Cyrtophora hirta</i> L. Koch 1872	6.0 (4)	0
<i>Cyrtophora moluccensis</i> (Doleschall 1857)	10.9 \pm 4.1 (84)	0.2 \pm 0.2
Pinkenba		
Orb only		
<i>Araneus eburnus</i>	4.0 \pm 0.7 (1)	0
<i>Argiope</i> sp.	5.5 (1)	1.0
<i>Eriophora transmarina</i>	4.9 \pm 0.9 (68)	0.02 \pm 0.01
<i>Leucauge</i> sp.	5.9 \pm 1.2 (22)	0
Orb & Barrier		
<i>Nephila plumipes</i>	10.7 \pm 3.6 (116)	5.9 \pm 0.3
Orb & Tangle		
<i>Cyrtophora hirta</i>	4.0 \pm 2.1 (3)	2.0 \pm 1.7
<i>Cyrtophora moluccensis</i>	8.3 \pm 4.1 (5)	6.0 \pm 1.7
Yeppoon		
Orb only		
<i>Araneus dimidiatus</i>	5.4 \pm 1.1 (36)	0.1 \pm 0.1
<i>Gasteracantha</i> sp.	4.3 \pm 0.9 (10)	0
Orb & Barrier		
<i>Nephila pilipes</i> (Fabricius 1793)	21.3 \pm 11.5 (7)	0.6 \pm 0.4
<i>Nephila plumipes</i>	16.5 (1)	0
Orb & Tangle		
<i>Cyrtophora</i> sp.	6.3 \pm 1.2 (8)	0
Cairns		
Orb only		
<i>Araneus dimidiatus</i>	4.9 \pm 0.8 (311)	0.2 \pm 0.1
<i>Argiope</i> sp.	10.7 \pm 2.9 (33)	0.3 \pm 0.2
<i>Eriophora transmarina</i>	4.4 \pm 0.5 (13)	0
<i>Gasteracantha</i> sp.	5.9 \pm 1.8 (20)	0
<i>Leucauge</i> sp.	4.8 \pm 1.2 (20)	0
Orb & Barrier		
<i>Nephila pilipes</i>	12.8 \pm 10.9 (20)	0.4 \pm 0.3
<i>Nephilengys</i> sp.	5.6 \pm 1.8 (13)	0
Orb & Tangle		
<i>Cyrtophora</i> sp.	10.0 \pm 2.8 (5)	3.5 \pm 1.5

Table 2.—Average number of individuals of each species of *Argyrodes* per web (\pm standard error) at Everton park (south-east Queensland), Pinkenba (south-east Queensland), Yeppoon (central-east Queensland) and Cairns (far north Queensland).

Species	Everton Park	Pinkenba	Yeppoon	Cairns
<i>A. antipodianus</i>	1.40 \pm 0.19	3.36 \pm 0.24	0.12 \pm 0.05	0.19 \pm 0.05
<i>A. rainbowi</i>	0.13 \pm 0.04	0.03 \pm 0.01	—	—
<i>A. species 1</i>	0.22 \pm 0.07	0.03 \pm 0.01	0.01 \pm 0.01	—
<i>A. fissifrons</i>	0.09 \pm 0.04	—	—	—
<i>A. miniaceus</i>	—	—	0.22 \pm 0.12	0.25 \pm 0.08
<i>A. kulczynski</i>	—	—	0.24 \pm 0.08	0.01 \pm 0.01

in the four surveys, and *A. antipodianus* was associated with eight of the 12 host species sampled (Table 1). Only webs of *Araneus eburnus* (Keyserling 1886), *Gasteracantha* sp., *Leucauge* sp. and *Nephilengys* sp. had no *A. antipodianus*; however, for some of these hosts (e.g., *Nephilengys* sp.) very few webs were found (Table 1). Webs of *Araneus dimidiatus* (L. Koch 1871), present at every site except Pinkenba, consistently had low numbers of *A. antipodianus*, in spite of the high abundance of this host species (Table 1). Similarly, webs of *Eriophora transmarina* (Keyserling 1865), although relatively common in the southeastern Queensland sites, had very few *A. antipodianus* (Table 1). There was no apparent linear relationship between density of hosts (no. per 10,000 m²) and the mean number of *A. antipodianus* per web across all four sites ($R^2 = 0.02$; $F_{1,25} = 0.53$, $P = 0.47$), although spiders belonging to *Nephila* spp. and *Cyrtophora* spp., were clearly the preferred hosts (Table 1).

At Everton Park and Pinkenba, *A. antipodianus* was over six times more abundant than any other species of *Argyrodes*; however, in tropical Queensland (Cairns and Yeppoon) other species of *Argyrodes* were more abundant (Table 2). In Cairns, *A. miniaceus* (Dolschall 1857) was more numerous, while Yeppoon was dominated by *A. miniaceus* and *A. kulczynski* (Roewer 1942). Three additional species of *Argyrodes* (*A. fissifrons* O.P.-Cambridge 1869, *A. rainbowi* (Roewer 1942) and *Argyrodes* sp. 1) were also collected. In the presence of other species of *Argyrodes*, the abundance of *A. antipodianus* (2.6 \pm 0.5 spiders per web) was somewhat higher than that on webs with no congeners, although the difference was not significant (1.8 \pm 0.1 spiders per web; ANOVA: $F_{1,745} = 2.83$, $P = 0.093$).

Both body length and orb diameter of host spiders showed a positive linear relationship with the numbers of *A. antipodianus*. When data from all surveys were pooled, host length accounted for 28% of the variance in *A. antipodianus* numbers ($F_{1,742} = 286.5$, $P < 0.0001$). Orb diameter seemed to impose an upper limit on the numbers of the kleptobiont (Fig. 4: broken line), although the two variables were not strongly related ($R^2 = 0.13$; $F_{1,745} = 107.3$, $P < 0.0001$). Orb diameter also showed a positive relationship with the body length of hosts ($R^2 = 0.60$; $F_{1,742} = 1118.6$, $P < 0.0001$).

Species of *Nephila* and *Nephilengys* construct webs that consist of a vertical orb and a non-viscid barrier (Fig. 2). *Cyrtophora* spp. make non-viscid, horizontal orbs with an extensive tangle (Levi 1978; Shear 1994; Fig. 3). Spiders that construct webs consisting almost exclusively of a catching orb with little or no barrier include *Araneus dimidiatus*, *A. eburnus*, *Argiope* sp., *Eriophora transmarina*, *Gasteracantha* sp. and *Leucauge* sp..

Architecture of host webs (Fig. 1) influenced the abundance of *A. antipodianus* (ANOVA: $F_{1,745} = 217.04$, $P < 0.0001$). When all data were pooled, webs containing orbs with barriers had the highest numbers of the kleptobiont (mean of 4.6 \pm 0.3/web). Generally, orbs with a tangle had intermediate numbers of *A. antipodianus* (1.5 \pm 0.5/web) and webs that consisted only of orbs had the lowest numbers (0.09 \pm 0.02/web). In Cairns webs with orb and tangle had the most *A. antipodianus*, although these results applied only to two individuals of an unidentified species of *Cyrtophora*.

Abundance of *A. antipodianus* on webs of *N. plumipes*.—At Pinkenba we examined a total of 299 webs in the survey of all stages

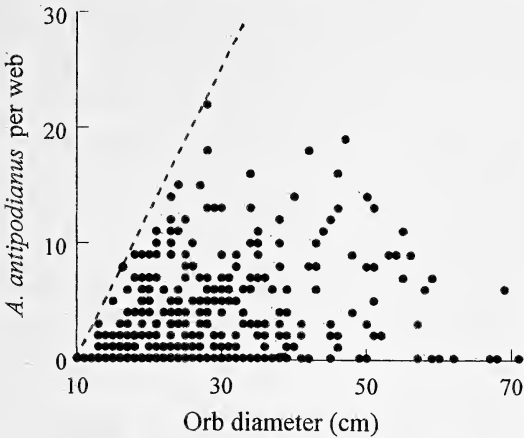


Figure 4.—Numbers of *Argyrodes antipodius* per web against orb diameter (cm) of host webs at Everton Park, Pinkenba, Yeppoon and Cairns.

of *N. plumipes* and 213 webs in the survey of adult *N. plumipes*. There was an average of 5.7 ± 0.3 *A. antipodius* per web in the former and 2.3 ± 0.1 in the latter census. Numbers of *A. antipodius* were positively related with the width of host carapace, although, as in the across-species comparison, this relationship was not strong for all host stages ($R^2 = 0.27$; $F_{1,297} = 109.7$, $P < 0.0001$) or adult hosts ($R^2 = 0.15$; $F_{1,211} = 36.18$, $P < 0.0001$). Orb diameter of *N. plumipes* showed a similar pattern of relation with the abundance of *A. antipodius* (all hosts $R^2 = 0.22$, $F_{1,297} = 85.95$, $P < 0.0001$; adult hosts $R^2 = 0.12$, $F_{1,211} = 28.44$, $P < 0.0001$).

Our visual estimation of the complexity of the barrier (categories 0 to 4) was sufficiently accurate, since the ratios of orb weight/barrier weight (\pm SE, $n = 10$) differed between categories (category 1 = 0.1 ± 0.02 ; 2 = 0.3 ± 0.1 ; 3 = 1.1 ± 0.4 ; 4 = 1.9 ± 0.5). Nevertheless, barrier complexity did not have an effect on *A. antipodius* in either survey (AN-

OVA, all webs $F_{4,289} = 1.44$, $P = 0.221$; adults only $F_{3,209} = 0.36$, $P = 0.786$).

Aggregation (\pm , recorded only for adult webs) did not affect the numbers of *A. antipodius* (ANOVA, $F_{1,211} = 2.13$, $P = 0.146$). However, abundance of these kleptobionts was over 65% higher on webs that had male *N. plumipes*. This result was highly significant for the survey of all stages of *N. plumipes*, with 9.0 ± 1.0 *A. antipodius* on webs with males ($n = 24$), and 5.5 ± 0.3 kleptobionts on webs without males ($n = 275$; ANOVA: $F_{1,297} = 15.78$, $P < 0.001$) and for the census of adult hosts (Fig. 5; ANOVA: $F_{1,211} = 7.96$, $P = 0.005$).

Retention of *A. antipodius* on webs of *N. plumipes*.—On average, after 24 hours, large webs (32 ± 4 cm diameter) built by adult *N. plumipes* retained over 85% more *A. antipodius* than small webs (18 ± 3 cm diameter), built by juvenile hosts (ANOVA, $P < 0.0001$; Fig. 6, Table 3). However, the presence of hosts on webs was of no consequence to the kleptobiont (ANOVA, $P = 0.895$; Table 3). When juvenile hosts were excluded, six of the twelve webs were destroyed or damaged by more than 30% by *A. antipodius* (pers. obs.), and were not included in the analysis. Webs of adult *N. plumipes* did not differ in shape or architecture from those built by the juveniles.

DISCUSSION

Kleptobiotic *Argyrodes* may be found on a range of webs (Kaston 1965; Elgar 1993), although they are likely to be more abundant on webs that are easy to forage on, supply sufficient food and provide ample refuge. Whitehouse (1988) found that in New Zealand *A. antipodius* specialized on a single host species, *Eriophora pustulosa*, in whose webs it foraged most efficiently. We have unpublished data that is consistent with Whitehouse

Table 3.—Two-way ANOVA for the effect of web size and presence of *N. plumipes* on the numbers of *A. antipodius* retained on webs after 24 hours in the greenhouse (initial number of kleptobionts per web = 10).

Category	df	MS	F	P
Web size	1	0.903	51.00	<0.0001
Host presence	1	0.0003	0.02	0.895
Web size * host pres.	1	0.021	1.19	0.282
Residual	38	0.02		



Figure 5.—Average number of *Argyrodes antipodius* per web on webs of adult *Nephila plumipes* females that included (males +), or did not include male hosts (males -).

(1988), i.e., other webs such as tangle webs constructed by theridiids (e.g., *Latrodectus* spp.) or space webs made by amaurobids (e.g., *Badumna* spp.) were rarely colonized by *A. antipodius* (P.G., pers. obs.). However, we also found that the kleptobiont has a broad host distribution, perhaps because our sampling areas had a higher diversity of web spiders than those examined by Whitehouse (Elgar 1993). Additionally, we found some evidence of web specificity by this kleptobiont, as it was found primarily on orb webs that included a scaffold (barrier or tangle): those of *Nephila* and *Cyrtophora* species.

Elgar (1993) pointed out that host specificity is likely to vary continuously and can be influenced by the abundance and diversity of hosts. Our data show that relative abundance of webs of each host species was not significantly correlated with the abundance of *A. antipodius*. However, availability of hosts probably does affect host choice by the kleptobiont. For example, *Eriophora pustulosa* were the preferred hosts in New Zealand during summer (Whitehouse 1988), but these were the only orb weavers present in the study site. On the other hand, in the presence of more complex orb webs (with scaffold) in Queensland, orb weavers that construct simple orb webs similar to *E. pustulosa* had few or no *A. antipodius*.

If kleptobiotic *Argyrodes* have a negative effect on their hosts, then web characteristics that favor them will carry a disadvantage to

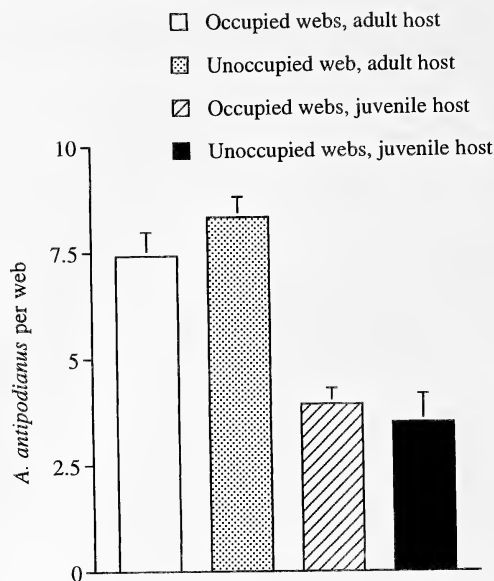


Figure 6.—Effects of web size and host presence on the retention of *Argyrodes antipodius* (number remaining after 24 hours) on webs of *Nephila plumipes* in the greenhouse. Data presented as means + standard error.

the web owner and may be under conflicting selective pressures (e.g., larger webs might catch more food, but may also increase the kleptobiont load). Elgar (1989) found that the intensity of infestation of *Nephila edulis* (Labillardiere 1799) webs by *A. antipodius* was correlated with host size. Our data show a positive correlation between the number of these kleptobionts and both host size and orb diameter, although little of the variance is explained (13–28%). This may be because host size or orb diameter is not always clear indicators of web size for spiders that construct webs of varying architecture. For instance, while orbs built by *Cyrtophora* (orb & tangle) are small, those of *Nephila* (orb & barrier) are large relative to total web space (Figs. 2, 3). Further, our results could have been confounded by survey site, season and species of host, which were all pooled. However, the correlation did not improve when we controlled for variation in web architecture, site and host species by using only *N. plumipes*. Nevertheless, orb size may impose an upper limit on the numbers of *A. antipodius* on host webs: large orbs may accommodate few or many *A. antipodius*, but small orbs contain only few kleptobionts. This was supported by our data

from the greenhouse, which showed that independent of host presence, small webs (juvenile *N. plumipes*) retain fewer *A. antipodanus* than large webs (adult hosts).

Although we examined 512 webs in our surveys of *N. plumipes*, we did not find an obvious effect of web architecture or aggregation on the numbers of *A. antipodanus*; and perhaps the distribution of this kleptobiont is more random than previously hypothesized (Elgar 1989). However, apart from the structural characteristics of webs that we measured, several other factors may directly influence the number of *A. antipodanus* on webs. These could include the web tenacity of hosts (Levi 1978), food abundance and quality, host behavior and environmental factors, all of which ought to be examined in future studies.

Contrary to our hypothesis that other web visitors might have a damping effect on numbers of *A. antipodanus*, the presence of other *Argyroides* had no significant effect. Also, surprisingly, male hosts were associated with greatly elevated numbers of this kleptobiont, as there were two-thirds more *A. antipodanus* on webs of female *N. plumipes* colonized by males, than on webs with no males. We offer two alternative hypotheses to explain this unexpected result. First, both males and kleptobionts may be responding to the same factors, e.g., food availability, position in wind corridors or insolation. Also, pheromones emitted by female hosts can be perceived not only by the males, but perhaps also by the kleptobionts, consequently facilitating web location. Second, the activity of *Nephila* males (including feeding and mating attempts) may be beneficial to *A. antipodanus* through disturbance of the web and distraction of the female host. Thus, with males present, *A. antipodanus* would face lower levels of aggressive response by the web owner, and perhaps have a higher foraging success, thus remaining on the web longer. Possibly, *A. antipodanus* engages in "smokescreening" behavior (Wilcox et al. 1996) by increasing its feeding while female hosts are distracted. If mating attempts of male *N. plumipes* cause higher infestation levels of kleptobionts, then reproduction of this host may come at a previously unnoticed cost.

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ABUNDANCE OF SPIDERS AND INSECT PREDATORS ON GRAPES IN CENTRAL CALIFORNIA

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ABSTRACT We compared the abundance of spiders and predaceous insects in five central California vineyards. Spiders constituted 98.1% of all predators collected. More than 90% of all spiders collected were from eight species of spiders, representing six families. Two theridiids (*Theridion dilutum* and *T. melanurum*) were the most abundant, followed by a miturgid (*Cheiracanthium inclusum*) and an agelinid (*Hololena nedra*). Predaceous insects comprised 1.6% of all predators collected, and were represented by six genera in five families. *Nabis americanus* (Heteroptera, Nabidae) was the most common predaceous insect, with its densities highest late in the growing season. *Chrysoperla carnea*, *Chrysoperla comanche* and *Chrysopa oculata* (Neuroptera, Chrysopidae) and *Hippodamia convergens* (Coleoptera, Coccinellidae) were most abundant early in the season. The dominance of spiders may be due to their more stable position in the vineyard predator community compared to predaceous insects. We also suggest that the low percentage of predaceous insects (e.g., lacewings) may reflect the lack of preferred prey (e.g., aphids) on grapevines.

Spiders are important predators in agroecosystems (reviews in Nyfeller & Benz 1987; Nyfeller et al. 1994). Many researchers have provided descriptions of spider species abundance or composition in a variety of agroecosystems (e.g., Bishop 1980; Dean et al. 1982; Agnew & Smith 1989; Bardwell & Averill 1997; Wisniewska & Prokopy 1997). Other researchers have provided qualitative observations on the abundance of spiders (Carroll & Hoyt 1984) or recorded spider predation events (Reichert & Bishop 1990; Nyfeller et al. 1992). However, it is less common for researchers to compare spider abundance to that of predaceous insects. Those studies that have analyzed the relative abundance of all predaceous arthropods vary considerably in the presentation of the data. For example, MacLellan (1973) reported on predaceous arthropods collected on apples in southeastern Australia, presenting numbers of spiders collected by size and numbers of predaceous insects collected by family. Plagens (1983) re-

ported population densities of the most abundant spiders (*Misumenops* spp.) found on Arizona cotton, presenting predaceous insects as overall percentages but not itemizing for different taxonomic groups. In these publications, the amount of detail presented reflects the focus of the research, depending in part upon the breadth of the predator taxon being studied. More commonly, researchers present more detailed descriptions of the predaceous insect fauna, while spiders are grouped together and data presented as an overall mean, numerical rank or percentage of the number collected (e.g., Roach 1980; Knutson & Gilstrap 1989; Royer & Walgenbach 1991; Braman & Pendley 1993). Few studies have provided equivalent comparisons of spiders and predaceous insects at the genus or species level (but see Breene et al. 1989).

In vineyards, several researchers have cataloged the abundance of predaceous arthropods on grapevines. In southern Germany, Buchholz & Schruft (1994) presented numbers of predaceous insects by family, identifying salticids to species and thomisids to genus, but leaving most spiders unidentified. In California vineyards, spider species composi-

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tion, relative abundance and seasonal occurrence were described by Costello & Daane (1995) and Roltsch et al. (1998), but neither study included data on predaceous insects. Here, we present data that compare the relative abundance of spiders to predaceous insects on grapevines in California's central valley.

METHODS

Study sites.—The data presented are from five central valley vineyards that were sampled from 1995–1997. Grapevine cultivar and cultural practices varied among the sites. In 1995, three vineyards in Fresno County were sampled: a raisin vineyard (*cultivar* “Thompson Seedless” near Del Rey, California) a table grape vineyard (*cultivar* “Ruby Seedless” near Reedley, California) and a juice vineyard (*cv* “Thompson Seedless” near Parlier, California). In 1995 and 1996, a winegrape vineyard in San Joaquin County (*cv* “Cabernet Sauvignon” near Woodbridge, California) and, in 1996 and 1997, a juice vineyard in Madera County were sampled (*cv* “Thompson Seedless” near Ripperdan, California). These sites were part of studies designed to determine the impact of cover crops on vineyard insect pests and their natural enemies (see Costello & Daane 1998b; Daane & Costello 1998). All of the study sites were bordered by cultivated vineyards or orchards.

In each year, all vineyards received multiple applications of sulfur for control of powdery mildew, *Uncinula necator* Burrill, and one or two applications of cryolite (sodium aluminofluoride) for control of omnivorous leaf-roller, *Platynota stultana* Walshingham 1884 (Lepidoptera, Tortricidae), and grapeleaf folder, *Desmia funeralis* (Hübner 1796) (Lepidoptera, Pyralidae).

Sampling.—Costello & Daane (1997) provide a detailed description of sampling methods. In brief, the Del Rey, Ripperdan, Parlier and Woodbridge vineyards were sampled by shaking a 0.89 m² section of vine foliage into a funnel shaped collector, and the Reedley vineyard was sampled by shaking the foliage of two grapevines onto a drop cloth and collecting all predators with small battery-powered vacuums. Samples were taken monthly, from May to September, except for the Ripperdan vineyard in 1996, which was sampled from July to September. On each sampling

date, samples were taken between 0700–1200 h PDT. Samples from the replicated cover crop studies were pooled across treatments and sample dates. A total of 100 samples was taken from the Reedley vineyard, 180 from the Del Rey vineyard and 120 from the Parlier vineyard (one season each). A total of 243 samples was taken from the Ripperdan vineyard and 360 from the Woodbridge vineyard (two seasons each). Voucher specimens were deposited at the Essig Museum at the University of California at Berkeley.

For each vineyard and sampling method, means were transformed to numbers of predators per vine. Seasonal abundance of spiders and predaceous insects were plotted against cumulative degree days above 10 °C (the lower developmental threshold for grapevines) from 1 January, for each sample year.

RESULTS

We collected a total of 13,348 spiders (2781 at Del Rey, 6468 at Woodbridge, 1273 at Ripperdan, 679 at Parlier and 2147 at Reedley) and 219 predaceous insects (36 at Del Rey, 122 at Woodbridge, 6 at Ripperdan, 43 at Parlier and 12 at Reedley). Over all sites, spiders constituted 98.1% of all predators collected, whereas the insect predators comprised just 1.6% of total predators. At individual sites, spiders comprised at least 94% of predators collected, with the highest percentage at Ripperdan (99.5%) and the lowest at Parlier (94.0%) (Table 1). Predaceous insects comprised 6.0% or less of all predators at each site, the highest percentage found at Parlier (5.9%) and the lowest at Ripperdan and Reedley (0.5%) (Table 1). The only other arthropod predator collected was *Anystis agilis* (Banks 1915) (Acari, Anystidae), a predaceous mite that feeds on insects as opposed to spider mites. Only 17 *Anystis agilis* were collected, all at the Reedley site, comprising 1.5% of the predators collected there.

Spiders.—Eight species from six families constituted >90% of all spiders collected. By family, these were: (1) Miturgidae: *Cheiracanthium inclusum* (Hentz 1847); (2) Corinnidae: *Trachelas pacificus* (Chamberlin & Ivie 1935); (3) Theridiidae: *Theridion dilutum* Levi 1957 and *Theridion melanurum* Hahn 1831; (4) Oxyopidae: *Oxyopes scalaris* Hentz 1845 and *Oxyopes salticus* Hentz 1845; (5) Agelinidae: *Hololena nedra* Chamberlin &

Table 1.—Mean season-wide density and population percentage of predatory arthropods in five central valley vineyards, 1995–97, data pooled across years for each site. Superscript “1” indicates *Theridion dilutum* and *Theridion melanurum*. Superscript “2” indicates *Oxyopes scalaris* and *Oxyopes salticus*.

Predator Group	Ripperdan Mean (±SE)	%	Woodbridge Mean (±SE)	%	Del Rey Mean (±SE)	%	Reedley Mean (±SE)	%	Parlier Mean (±SE)	%
Araneae										
<i>Theridion</i> spp. ¹	7.85 (1.06)	36.20	28.76 (2.24)	57.20	22.40 (2.37)	41.28	0.32 (0.67)	2.96	3.26 (0.74)	14.66
<i>Cheiracanthium</i> <i>inclusum</i>	4.79 (0.34)	22.04	11.27 (0.75)	22.41	4.06 (0.40)	7.49	0.45 (0.06)	4.05	4.92 (0.69)	22.13
<i>Trachelas pacificus</i>	1.54 (0.28)	7.11	0.20 (0.06)	0.40	4.00 (0.45)	7.38	4.53 (0.47)	41.35	4.27 (0.62)	19.22
<i>Hololena nedra</i>	5.75 (0.41)	26.50	0.55 (0.09)	1.09	16.95 (1.24)	31.23	1.85 (0.19)	16.87	1.04 (0.19)	4.70
<i>Oxyopes</i> spp. ²	0.92 (0.18)	4.22	1.84 (0.24)	3.65	1.59 (0.27)	2.94	1.33 (0.20)	12.17	0.21 (0.09)	0.97
<i>Metaphidippus vitis</i>	0	0	0	0	0.67 (0.13)	1.24	0.84 (0.09)	7.61	4.89 (0.59)	21.87
<i>Erigone dentosa</i>	0.12 (0.04)	0.55	4.66 (0.61)	9.28	3.23 (0.56)	5.95	0.25 (0.05)	2.27	1.26 (0.24)	5.63
Other spiders	0.39 (0.09)	2.34	1.84 (0.15)	3.65	0.67 (0.12)	1.24	1.24 (0.10)	10.66	1.17 (0.20)	5.22
Spider total	21.62 (1.48)	99.53	49.14 (2.74)	97.72	53.57 (3.54)	98.72	10.73	97.90	20.90 (1.92)	94.08
Acari										
<i>Anystis agilis</i>	0	0	0	0	0	0	0.17 (0.08)	1.54	0	0
Insecta										
<i>Hippodamia convergens</i>	0.017 (0.016)	0.08	0.19 (0.04)	0.38	0.23 (0.06)	0.42	0.03 (0.02)	0.32	0.12 (0.06)	0.55
Chrysopidae	0.017 (0.016)	0.08	0.55 (0.08)	1.09	0.21 (0.06)	0.39	0.01 (0.01)	0.09	0.12 (0.06)	0.55
<i>Nabis americana</i>	0.017 (0.016)	0.08	0.22 (0.09)	0.44	0.23 (0.09)	0.42	0.01 (0.01)	0.09	0.83 (0.29)	3.73
<i>Orius</i> spp.	0.034 (0.023)	0.16	0.06 (0.02)	0.13	0.02 (0.02)	0.03	0	0	0.09 (0.05)	0.41
<i>Geocoris</i> spp.	0.017 (0.016)	0.08	0.01 (0.01)	0.02	0	0	0	0	0.09 (0.07)	0.41
<i>Zelus renardii</i>	0	0	0.04 (0.02)	0.09	0	0	0	0	0	0
<i>Tenodera aridifolia</i> <i>sinensis</i>	0	0	0.04 (0.02)	0.09	0	0	0.005 (0.005)	0.05	0.06 (0.06)	0.27
Insect predator total	0.101 (0.040)	0.47	1.14 (0.12)	2.27	0.69 (0.13)	1.28	0.06 (0.02)	0.56	1.32 (0.33)	5.92

Ivie 1942; and (6) Salticidae: *Metaphidippus vitis* (Cockerell 1895).

Overall spider abundance varied among sites, ranging from a high of 49.1 spiders per vine (Woodbridge site) to a low of 10.7 spiders per vine (Reedley site) (Table 1). Species composition also varied among sites and may have contributed to differences in spider abundance. For example, overall spider abundance was highest at the Del Rey and Woodbridge sites, where the dominant spiders were the small, web-building theridiids, *T. dilutum* and *T. melanurum*. In contrast, overall spider abundance was more than 50% lower at the other sites, where larger spiders, such as the nocturnal hunters *C. inclusum* and *T. pacificus*, dominated the spider community (Table 1).

There were also differences in spider seasonal abundance (Fig. 1). *Theridion* spp. was the most abundant spider group, with the highest overall spider density in both the early-season (~17 per vine) and late-season (~34 per vine) samples, but equivalent with *C. inclusum* in mid-season samples (~7.5 per vine). *Cheiracanthium inclusum* was the next most abundant spider, with densities relatively low early in the season (~2 per vine) and peaking late in the season (~18 per vine). The agelinid, *Hololena nedra*, maintained a relatively steady population density of ~4.7 spiders per vine throughout the season. The seasonal abundance patterns reported here are consistent with those reported in Costello & Daane (1995).

Insects.—Predaceous insects collected include *Hippodamia convergens* Guérin-Méneville 1842 (Coleoptera, Coccinellidae); *Chrysoperla comanche* Banks 1938, *Chrysoperla carnea* (Stephens 1836), and *Chrysopa oculata* Say 1839 (Neuroptera, Chrysopidae); *Nabis americanoferus* Carayon 1961 (Heteroptera, Nabidae); *Orius* spp. (Heteroptera, Anthracoridae); *Geocoris* spp. (Heteroptera, Lygaeidae); *Zelus renardii* Kolenati 1856 (Heteroptera, Reduviidae); and *Tenodera aridifolia sinensis* Saussure 1871 (Mantodea, Mantidae).

Overall, predaceous insect density was lowest at the Reedley and Ripperdan sites, with seasonal means of 0.06 and 0.10 predators per vine, respectively, and most abundant at the Woodbridge and Parlier sites, averaging 1.1 and 1.3 predators per vine, respectively (Table 1). There were also differences among sites in

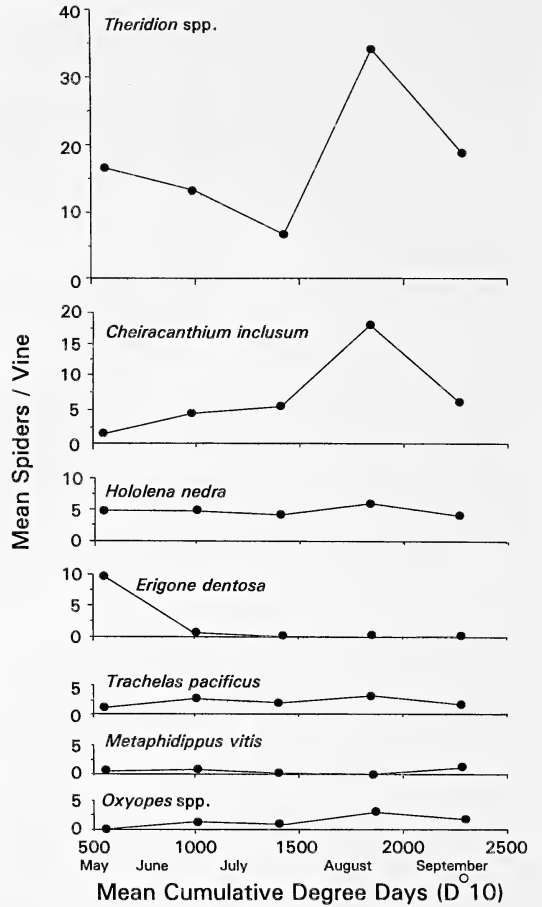


Figure 1.—Mean seasonal abundance of the most abundant spider species on grapevines, plotted against cumulative seasonal degree days above 10 °C (since January 1), all vineyards and years combined.

species composition. At the Woodbridge site, the most abundant insect predators were the chrysopids (0.5 per vine), whereas at the Parlier site, *N. americanoferus* was most frequently collected (0.8 per vine) (Table 1).

Predaceous insect seasonal patterns show that *N. americanoferus* was the most abundant insect predator overall (Fig. 2). Its population rose from near zero in early-season samples to ~0.6 per vine in late-season samples. Chrysopids were the most abundant predaceous insects in early-season samples, with densities of ~0.6 per vine, but thereafter were quite rare (Fig. 2). Coccinellidae were also relatively abundant in early-season samples (0.35 per vine at the first sampling period) and their density also steadily dropped in later samples.

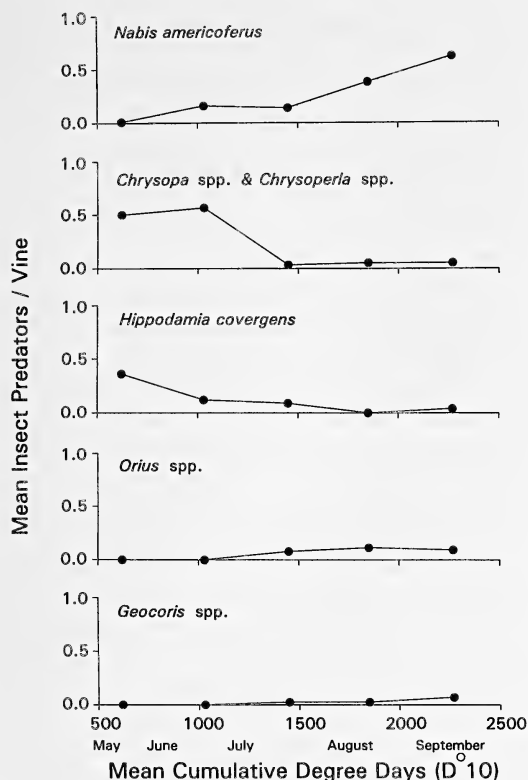


Figure 2.—Mean seasonal abundance of the most abundant predaceous insect groups on grapevines, plotted against cumulative seasonal degree days above 10 °C (since January 1), all vineyards and years combined.

Orius spp. and *Geocoris* spp. were not collected until the third sampling period (mid-summer), and peaked in late-season samples at 0.11 and 0.06 per vine, respectively.

DISCUSSION

These results show that spiders overwhelmingly outnumber predaceous insects on grapevines in California's central valley. The explanation for this may partly lie in the type and abundance of prey species: the low number of predaceous insects may reflect the lack of preferred prey on grapevines. At all of our study sites, the most abundant insects on grape foliage are various Diptera, which are most abundant in the spring and early summer, and the leafhoppers *Erythroneura elegantula* Osborn 1928 and *E. variabilis* Beamer 1929 (Homoptera, Cicadellidae). *Erythroneura* spp. have three generations in the central valley, with nymphal peaks occurring in late May,

mid-July and early September. Leafhopper densities which reach 10–15 nymphs per leaf may require insecticide treatment to prevent economic damage. In comparison, there were low densities of other potential arthropod prey, such as lepidopteran larvae (*Platynota stultana* and *Desmia funeralis*), mealybugs (*Pseudococcus maritimus* Ehrhorn 1900) and spider mites (*Tetranychus pacificus* McGregor 1919 and *Eotetranychus willametti* [McGregor 1917]). Prey such as aphids and whiteflies are only occasionally found on grapevines, and at relatively low densities.

Insect predators such as coccinellids and chrysopids will feed on a variety of soft bodied insects, including *Erythroneura* spp.; however, they are better known as predators of aphids and mealybugs (Daane et al. 1998). The lack of preferred prey likely affects the dispersal habits of adult coccinellids and chrysopids, and their density on grapevines. For example, migration of *Hippodamia convergens* from overwintering sites in the Sierra Nevada foothills to the San Joaquin Valley is arrested when adult beetles find aphids and their honeydew (Hagen 1962). Similarly, *Chrysopa carnea* responds to aphid honeydew (Hagen 1950). It is well known that cover crops such as vetches and cereals support high populations of aphids (Bugg et al. 1991), and we suspect that the relatively high early season populations of *H. convergens* and chrysopids we found on the grapevines were due to the presence of aphids on cover crops and weeds in and around the study vineyards at that time. The decline of these predators, during the season, followed the decline of their preferred prey on the cover crops.

Although spiders are polyphagous, we found differences among vineyard species in prey preference. For example, *Metaphidippus vitis* does not feed on leafhoppers in the laboratory; and, in this study, its numbers were relatively low compared with other spider species. In contrast, field observations suggest that *Theridion* spp. feed primarily on leafhoppers, with high populations of *Theridion* positively correlated with high leafhopper densities (Costello & Daane 1995). In this study, *Theridion* spp. reached the highest density of any spider group. *Theridion* spp. numbers were highest at the Woodbridge and Del Rey sites, where there were also high population levels of leafhoppers (Daane & Costello

1998). *Theridion dilutum* and *T. melanurum* are small (adults are ~0.5 cm), have low food requirements, occupy very little territory compared to larger spiders such as *Cheiracanthium inclusum* and *Hololena nedra*, and *Theridion* spp. populations increase considerably from mid- to late-summer. Therefore, *Theridion* spp. densities may be highest because they readily feed on leafhopper nymphs and because grapevines can support more of these spiders per given area compared with other spider species.

That nabids increased over the course of the season may reflect their ability to use leafhoppers as food. Nabids are good predators of leafhoppers (Martinez & Pienkowski 1982; Flinn et al. 1985). Other insect predators, such as *Orius* spp., prefer thrips and spider mites. *Geocoris* spp. feed on lepidopteran and hemipteran eggs and nymphs, spider mites, aphids and whiteflies (Hagler & Cohen 1991). The low densities of these prey items on vines may explain the low density of *Orius* and *Geocoris* species we found.

Spiders may also comprise the majority of the predator community because most species overwinter in the vineyard and are therefore permanent residents. They are a more stable part of the predator community than insect predators because of their broader diet breadth and their ability to subsist for long periods of time without food. Insect predators such as *Hippodamia convergens* and chrysopids are more migratory, and often follow migratory pest populations. All but one of the spiders mentioned in this study have been found overwintering in cardboard bands placed around the vine trunks, the exception being *Erigone dentosa* (M.J. Costello & K.M. Daane unpubl. data). None of the predaceous insects has been found overwintering on the vines. That *E. dentosa* was not found overwintering in vineyards and was only found in the early part of the growing season, suggests that it is more migratory than the other spider species, probably ballooning into vineyards in the spring and leaving for other habitats during the summer.

Finally, the sampling methods used will affect the kinds and numbers of predators collected. Costello & Daane (1997) compared the D-vac to foliage beating in vineyards, and found that spider density was underestimated by 87% with the D-vac, and overestimated by

35% with the funnel shake method. The D-vac also biased samples toward smaller and more mobile spiders compared to beating or shaking methods. In addition, foliage shaking methods do not collect flying predators. This is most important for the tiger fly, *Coenosia humilis* Meigen 1826 (Diptera, Muscidae), which can be quite common in San Joaquin Valley vineyards. The adult captures its prey on the wing and has been observed feeding on leafhopper adults (immature *Coenosia* feed on earthworms in the soil and, therefore, are not collected). We have collected this fly with the D-vac and have usually found the mean density to be less than 5 per vine (unpubl. data). In addition, very small predators such as *A. agilis* may never be sampled with the D-vac, and are probably more efficiently sampled with the drop cloth method than the funnel method. This may partly explain why an additional small insect predator, *Leptothrips mali*, was observed at the Woodbridge site but was never found in the samples.

This is the first report that spiders comprise such a high percentage of a predator community in vineyards. The great number of spiders in comparison to other predators reveal, empirically, why so much research has focused on spiders as vineyard predators (Zalom et al. 1993; Costello & Daane 1998; Roltsch et al. 1998). These results suggest that predaceous insects play a minor role in suppressing insect pest populations in California vineyards. We note that leafhoppers were the primary prey species in our study sites. In vineyards with high mealybug or lepidopteran populations, the natural densities of predaceous insects may be higher. More work is needed in determining the role of spiders on economically important vineyard insects such as leafhoppers and the lepidopteran complex. We are currently working on the development of immunochemical assays to estimate prey consumption by vineyard spiders.

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RESEARCH NOTE

UNUSUAL PHENOTYPE SUGGESTS ROLE FOR HOMEOTIC GENES IN ARACHNID DEVELOPMENT

Studies of segmental mutations in *Drosophila melanogaster* have led to the discovery of several classes of regulatory genes important in determining body pattern (Carroll 1995). These regulatory genes are also known as transcriptional factors because their proteins bind to another gene's control regions, or promoters, allowing for controlled expression or repression. For example, attachment of maternal effect gene transcripts to specific areas of an ovum in *Drosophila*, initiates the anterior-posterior (AP) body axis (Melton 1991). Diffusion of maternal effect proteins from opposing ovum poles creates a dual concentration gradient that differentially activates or represses additional classes of transcriptional factors. This cascade of regulatory gene expression determines positional information, indicating body polarity and regional specificity.

Regional specificity within body plans is largely determined by a class of transcriptional factors known as homeotic genes. Specific concentrations of maternal effect proteins turn on different homeotic genes controlling the identity of segments along the AP axis of an arthropod's body. Remarkably, homeotic genes are arranged on chromosomes in linear clusters corresponding to their exact sequence of expression. Those located toward the left end of the complex are expressed in posterior parts of the body, while those to the right are expressed toward the anterior parts (Kenyon 1994).

Bithorax (BX-C) and Antennapedia (ANT-C) are the two known complexes of homeotic genes. ANT-C in *Drosophila* controls the identity of appendages (Carroll 1995). A mutant ANT-C gene causes flies to grow a leg in their antennae socket. BX-C in *Drosophila* controls the morphology of the posterior thorax and abdomen. A mutant BX-C gene re-

sults in two rear-thoraxes instead of one front and one rear thorax, causing flies to have two pairs of wings instead of one pair of wings and one pair of halteres. In organisms other than *Drosophila*, genetic mechanisms underlying body plan development are less well understood and have only recently been investigated in arachnids (Damen et al. 1998; Telford & Thomas 1998).

Recently, I collected an immature *Misumenops* sp. (Thomisidae) on the Hawaiian Island of Maui which showed a dramatic segmental mutation. It was collected from wet forest in the Nature Conservancy's Waikamoi preserve on east Maui. This individual closely resembled *Misumenops anguliventris* Simon 1900, one of 17 described species of *Misumenops* endemic to the Hawaiian Islands. Thomisids are one of the few spider families containing genera that are known to be exceptionally diverse in the Hawaiian archipelago (Gillespie 1994).

After closer examination of this individual under a light microscope, I noticed a second set of eight eyes on its abdomen. These "abdominal eyes" displayed the exact pattern of the eight "normal" eyes on the cephalothorax. In addition, the dorsal aspect of the abdomen displayed the same type and pattern of setae also found on the carapace of the cephalothorax. Despite these dramatic morphological aberrations, the posterior aspect of the abdomen resembled a "normal" abdomen. At the time of collection, the spider was a third or fourth instar juvenile. It lived for two months and appeared typical in behavior. After death, the spider was preserved in 70% alcohol and was then prepared and examined using a Hitachi S-800 scanning electron microscope (see Figs. 1, 2). The specimen has been deposited in the Bishop Museum entomological collections.

Kaston (1982) summarized accounts of oc-



Figure 1.—Scanning electron micrograph of anomalous *Misumenops* sp. thomisid, dorso-lateral view.

ular anomalies in spiders. Of the nine cases he described, only two involved spiders gaining eyes. These specimens, having 14 and 16 eyes, were explained as a result of embryonic duplication of a head region. It is premature to suggest that these phenotypes were a result of a mutation in a major regulatory gene because there are no accompanying figures showing where these eyes were located. If additional eyes were located on a segment other than the cephalic, this confusion in segment identity would strongly suggest abnormal homeotic gene expression.

The “abdominal” eyes and duplicated setation pattern shown in the spider I collected may be explained by several different hypotheses. First, a mutation in a homeotic gene of the bithorax complex may account for the abnormal phenotype. However, homeotic mutations are expressed in individual segments and because spider abdomens are composed of several segments, generation of this phenotype would require independent mutations in all segments. It is more likely that this mutant was produced because the wrong set of homeotic genes was turned on, while the correct set was not. This could be brought about by several mechanisms. A mutation in a regulatory gene determining body polarity might

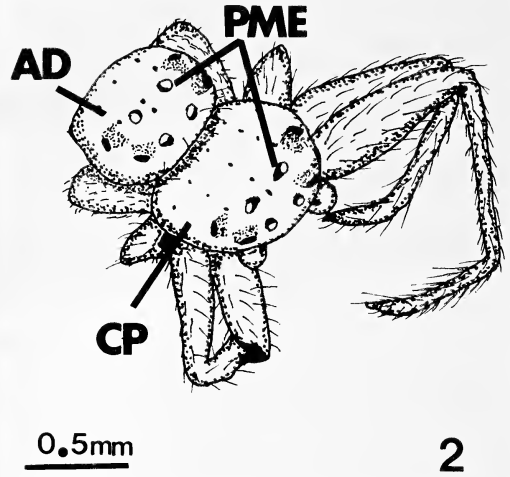


Figure 2.—Illustration of anomalous *Misumenops* sp. thomisid. PME = posterior median eyes, CP = cephalothorax, AD = abdomen.

turn on an entire group of regionally inappropriate homeotic genes. Alternatively, duplication of anterior structures might arise if maternal nurse cells placed transcripts activating anterior development at the anterior end of the ovum as well as the where the abdomen would normally arise. The mutant phenotype could also be created through a chromosomal aberration produced during gametogenesis. If the linear cluster of homeotic genes is duplicated at the region corresponding to the cephalothorax, this might result in the development of two cephalothoraxes.

Evolution of homeotic genes may explain the immense diversity of body forms seen among arthropods (Kenyon 1994; Carroll 1995). Small mutations in these highly conserved genes result in macro-mutations, providing an evolutionary mechanism for generating novel phenotypes. Homeotic genes have also been identified in cnidarians, nematodes and annelids. Most recently, homeotic genes have been identified in a spider (Damen et al. 1998) and mite (Telford & Thomas 1998). Comparative investigation of homeotic gene expression will undoubtedly play an important role in understanding the evolution of arachnid morphology.

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RESEARCH NOTE

NOMENCLATURE OF THE ORB-WEB

In science, we have to know what we are talking about when we say something. Unfortunately, in the literature about orb-webs and orb-web construction, different terms are used for the same part of the web and—even worse—the same term is used by different authors for different parts of the web. The present note tries to improve the situation by proposing a nomenclature for the different parts of the orb-web (Fig. 1). At the same time, an overview of the terms used by various other authors is given in English, German and French.

Anchor threads and frame threads.—The web is supported by anchor threads attached to the supporting structure at anchor points. The thread along the outside of the web is called the frame. The primary frame (thread) is attached on both ends to anchor threads and forms the outermost outline of the web. A secondary frame (thread) is attached to two primary frame threads that form a corner with each other (Mayer 1952). The point where two primary frame threads connect to an anchor thread is called a frame point. The (primary) frame thread along the top of the web is also called bridge thread—not to be confused with the bridging line, the thread the spider lets float in the breeze to cross open gaps (Peters 1989).

Radii.—The threads running more or less straight from the center of the web to the circumference are called radii. There are different kinds of radii, but not all authors make the same distinction among them. In the normal orb-web, as exemplified by that of *Araneus diadematus*, I propose to distinguish between proto-radii, primary radii and secondary radii. Some species additionally have subsidiary radii and others have accessory radii.

Proto-radii only exist during the early stages of web construction. They are threads between the proto-hub (hence the name for the

proto-radii) and the supporting structure. During the web building process, proto-radii are usually converted into (and partially replaced by) anchor threads (Eberhard 1990; Zschokke 1996). Primary radii are radii that are constructed simultaneously with a frame thread (primary or secondary); secondary radii are constructed without building a frame thread at the same time. When looking at a finished web, primary and secondary radii cannot readily be distinguished, although Wirth (1988) has been able to tell the difference by studying the fine structure of the connection between the radius and the frame thread. In Fig. 1, the distinction was based on the recording of the construction of the web. If the distinction between primary and secondary radii is not possible or not necessary, both can simply be named 'radius.'

Some spiders build subsidiary radii. Subsidiary radii are radii that do not start at the hub but somewhere further out: they are either attached to another radius (*Cyrtophora* sp.) or to the auxiliary spiral (*Nephila* sp.). Finally, some symphytognathoid spiders build accessory radii. Accessory radii are made after sticky spiral construction but before hub modification (Coddington 1986b; pers. comm.). They are distinct from normal radii by not being connected to the sticky spiral.

In the past, there has been a certain confusion about the use of the terms 'primary radius,' 'secondary radius' and 'tertiary radius'. 'Primary radius' has been used to designate what I call a proto-radius (Tilquin 1942; Coddington 1986a), to designate a radius constructed together with a primary frame thread (Mayer 1952), or—as proposed here—to designate a radius constructed simultaneously with a (primary or secondary) frame thread (Peters 1937b; Wirth 1988). The term 'secondary radius' has been used by several authors (Tilquin 1942; Mayer 1952; Savory

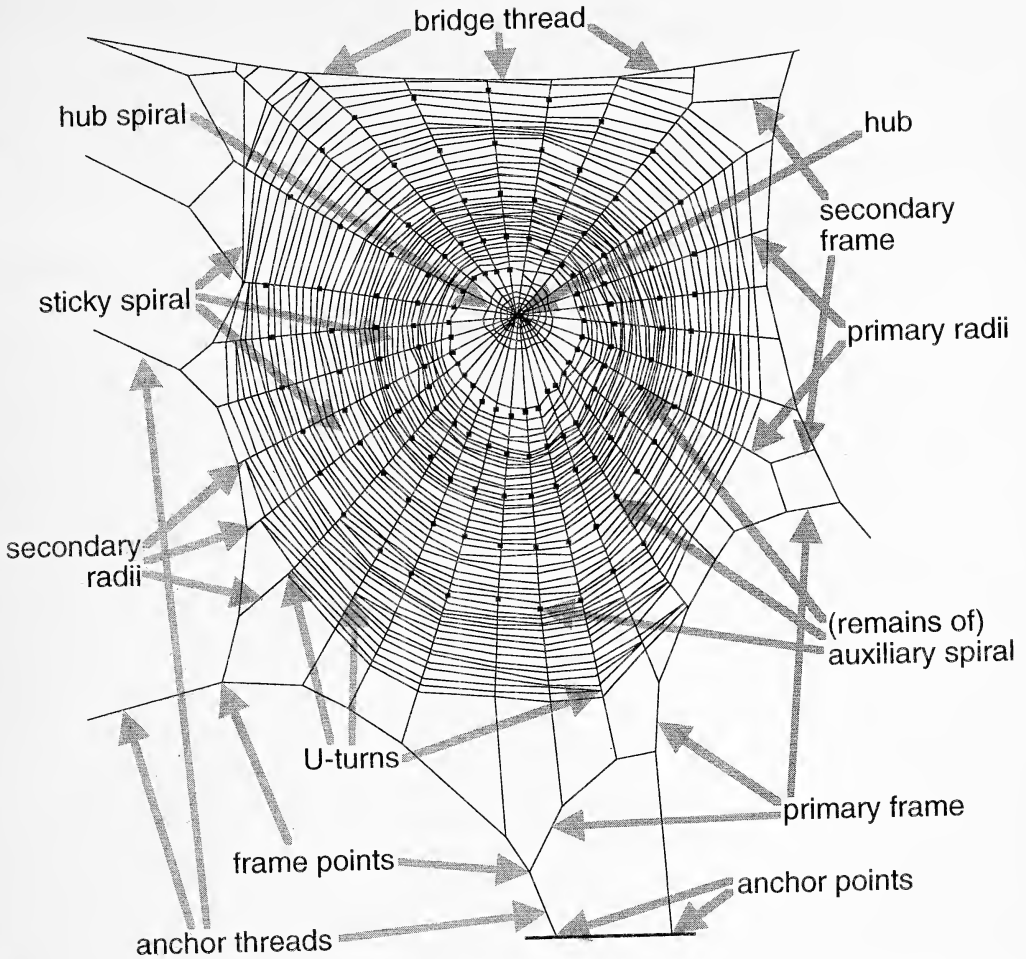


Figure 1.—Web of *Araneus diadematus* with the terms for its parts. See text for names of structures not found in the web of *Araneus diadematus* (e.g., retreat, stabilimentum).

1952) to designate a radius built at the same time as a (secondary) frame thread. Many authors (Peters 1937b; Wirth 1988; Vollrath 1992) have—as proposed here—used it to describe a radius built without a frame thread and some other authors (e.g., Shear 1986) have used it to describe what I call a subsidiary radius. The term ‘tertiary radius’ has been used to describe what I call secondary radius (Tilquin 1942; Mayer 1952; Vollrath 1992) or to describe what I call subsidiary radii (Eberhard 1972).

Jackson (1973) has devised an entirely different terminology to distinguish between different radii. His distinction is not based on the mode of construction but on the position in

the web, allowing the identification of each radius.

Spirals.—Spirals are the distinctive feature of orb-webs. Most orb-webs contain two major spirals: a spiral made out of sticky silk, the sticky spiral, and a spiral made out of non-sticky silk, the auxiliary spiral. The auxiliary spiral is removed by most spiders during construction of the sticky spiral and all that is left are small balls of silk along the radii (cf. Fig. 1). There are, however, webs of a few spiders (e.g., *Nephila* sp. and in parts of the web of *Scoloderus* sp.) where the auxiliary spiral remains in the completed web. Accordingly, some authors (e.g., Stern & Kullmann 1975) distinguish between a structural spiral (‘Festi-

Table 1.—List of proposed terms and terms used by other authors to designate certain parts of a spider's web. In English, some authors used the word 'line' or 'strand' in place of 'thread'.

Proposed term	Other terms in English	In German	In French
anchor points	mooring point	Anheftungspunkte Verankerungspunkte	
anchor thread	frame thread guy thread mooring thread	Ankerfaden Haltefaden Spannseil Tragseil Verankerungsfaden	fil d'attache
primary frame	foundation	Begrenzung Rahmen	cadre
secondary frame	auxiliary frame cord inner frame radial Y-structure section thread Y-frame	Sekundärer Rahmen Rahmen 2. Ordnung Hilfsrahmen	cadre secondaire
frame point bridge thread	frame Y-structure		
		Brückenfaden	cable suspenseur fil suspenseur
radius	radial radial thread radiating thread spoke ray	Radialfaden Radialspeiche Radius Speiche Stützfaden	diamètres rayon
proto-radius	primary radius	Ausgangsstrahlen Grundstrahlen	
primary radius secondary radius subsidiary radius	secondary radius tertiary radius secondary radius tertiary radius		
proto-hub hub	rudimentary hub	Nabe Warte	moyeu
sticky spiral	capture spiral catching spiral ensnaring spiral outer spiral permanent spiral viscid spiral	Fangspirale Klebfaden Klebspirale	fil spiralaire spire caprice spirale définitive spirale externe spirale gluante
auxiliary spiral	nonsticky spiral preliminary spiral primary spiral provisional spiral scaffolding spiral structural spiral temporary spiral	Festigungsspirale Gerüstspirale Hilfsspirale	spirale auxiliare spirale provisoire spirale sèche
hub spiral	inner spiral strengthening spiral	Befestigungsspirale	spirale interne
U-turn	loop (point of) reversal reverse switchback turnback turning point	Umkehrpunkt Umkehrstellen	coudes en épingle à cheveux grecques retour

Table 1.—Continued.

Proposed term	Other terms in English	In German	In French
signal thread	guide line to retreat	Signalfaden	fil avertisseur fil d'avertissement
retreat	hiding place	Schlupfwinkel Versteck Warte	demeure retraite refuge
stabilimentum		Stabiliment	stabilimentum in hub: revêtement

gungsspirale') which is left in the finished web as opposed to a temporary spiral which is removed during construction of the sticky spiral. Curiously, the term temporary spiral has also been used to describe the auxiliary spiral in webs where the auxiliary spiral is permanent (Eberhard 1975). The hub spiral is the innermost part of the auxiliary spiral which is not removed during construction of the sticky spiral.

Other structures.—In addition to frame, radii and spirals, some orb-webs contain additional structures. Some spiders do not sit on the hub when waiting for prey, but rather they sit hidden in the retreat (e.g., *Zygiella x-notata*). The signal thread connects the hub of the web with the retreat, allowing the spider sitting in the retreat to detect any vibrations occurring in the web and to dash to the center of the web without being slowed by the sticky spiral. Stabilimentum is the name for a variety of additional silk structures on the orb web (for an overview of the different kinds of stabilimenta, see Foelix 1996).

Terminology used by other authors and in other languages.—Table 1 gives an overview of the terms proposed in this note (first column) and the terms used by various other authors in English, German and French. The names are also given in German and French because many of the classic papers on spiders web were written in German (e.g., Wiehle 1927; Peters 1937a, 1937b; Mayer 1952) or in French (e.g., Tilquin 1942; Le Guelte 1964).

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RESEARCH NOTE

ON *SOFANAPIS ANTILLANCA* (ARANEAE, ANAPIDAE) AS A KLEPTOPARASITE OF AUSTROCHILINE SPIDERS (ARANEAE, AUSTROCHILIDAE)

Kleptoparasitic habits are well known in certain spiders, notably some mysmenids and members of the theridiid genus *Argyrodes* Simon 1864 (Elgar 1993). Members of the Dictynidae, Heteropodidae, Oonopidae, Salticidae, and Symphytognathidae have also been recorded as kleptoparasites of web-building spiders (Elgar 1993, table 1). We present here the first evidence of kleptoparasitism in the Anapidae, as well as the first report of a kleptoparasite associated with the primitive and relictual spider subfamily Austrochilinae.

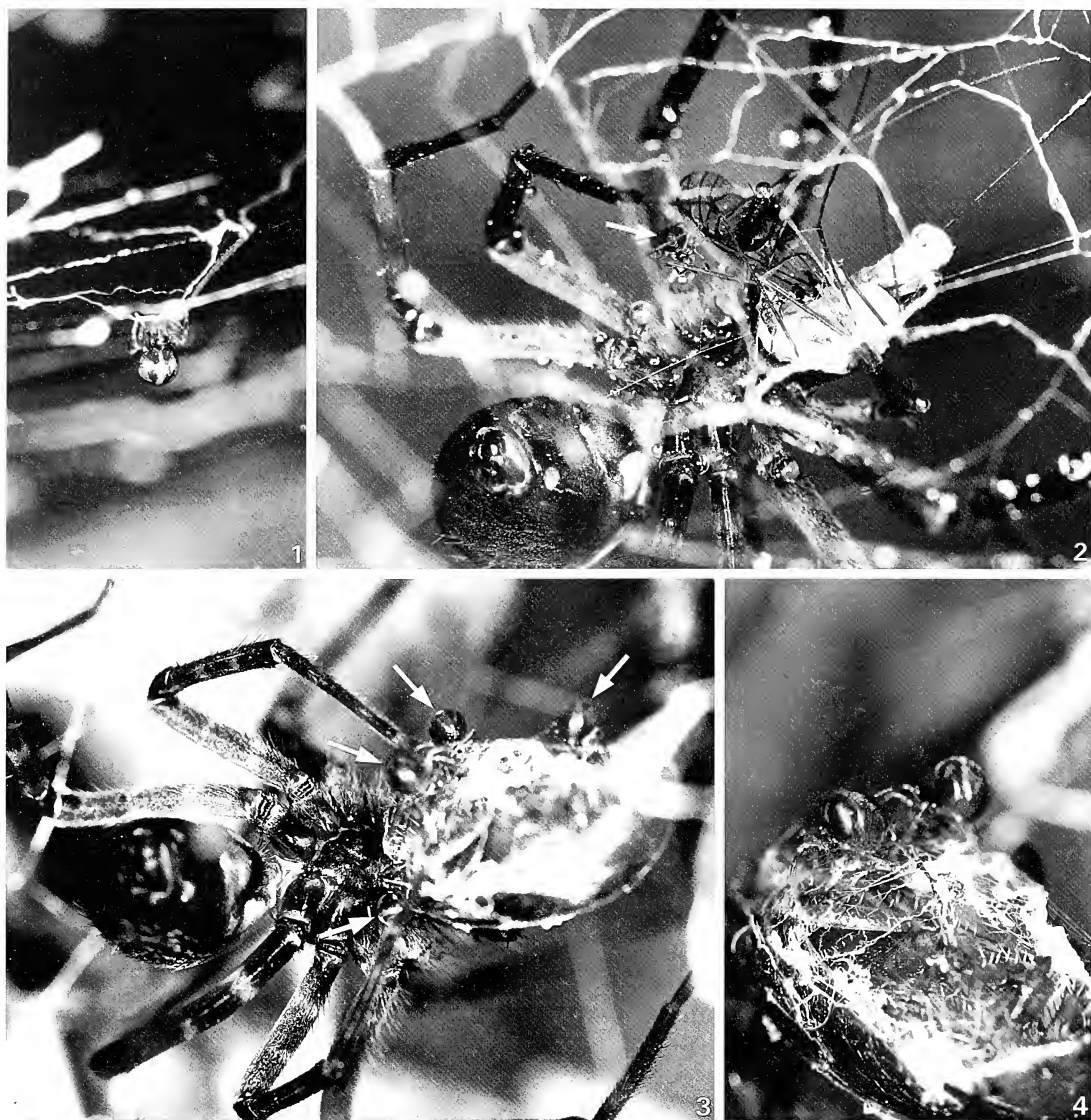
Austrochilines comprise two genera, *Austrochilus* Gertsch & Zapfe 1955 and *Thaïda* Karsch 1880, restricted to the temperate forests of Chile and adjacent Argentina. They build conspicuous, large (about 50–120 cm long), horizontal, aerial webs, consisting of a single layer of threads forming an irregular net (Forster et al. 1987; Zapfe 1955). The cribellate, whitish threads make the web easily visible. The horizontal net gradually bends into a concavity, forming a funnel that goes far back into log cracks, tree roots, or rocks, ending in a retreat where the spider rests during the day. At night, the spider hangs under its web and can be seen combing cribellate silk, or feeding. Large prey items, up to the spider's body size, are wrapped with silk before being eaten.

The retreats of adult females often contain much silk and several egg cases (Forster et al. 1987). The web is repaired when damaged; and the newly constructed patches, with bluish cribellate threads, are clearly discernible from the old portions, with powdered threads. Silk accumulation and web repair indicate that the web is persistent, a frequent characteristic of the hosts of kleptoparasites (Elgar 1993).

Sofanapis antillanca Platnick & Forster 1989 are very small spiders that were previously collected either by pyrethrin-fogging in

logs, or in Berlese samples of leaf litter and moss (Platnick & Forster 1989). During recent field work, we found some specimens on austrochiline webs, and after a systematic examination of webs, found evidence of kleptoparasitic behavior in these anapids. During the day, individuals of *S. antillanca* were collected on austrochilid webs (of both *Austrochilus* and *Thaïda* species), hanging from threads, rather deep in the mouth of the funnel, but still visible with a headlamp. At night, when the host is on its web, the anapids were mostly concentrated around the opening of the funnel, closer to the horizontal web. They hang from the host web's threads (Fig. 1), or more often, from an irregular mesh made of extremely fine threads. That mesh is presumably constructed by the *Sofanapis*, as it has not been found in non-infested webs. A web of an adult female of *Thaïda peculiaris* Karsch 1880 observed at Aguas Calientes in the Parque Nacional Puyehue, Osorno, Region X (Los Lagos), Chile, was found to host several specimens of *S. antillanca*, and in that web the thin (anapid) net was particularly dense. No orbwebs were found on any host web, nor was any insect found caught in the presumed anapid silk. Consequently, it seems that *S. antillanca* does not construct its own web for prey capture. The type specimens of *S. antillanca*, collected by pyrethrin fogging inside a rotten tree trunk (Platnick & Forster 1989), may actually have come from an austrochilid web.

A few hosts were observed while they were feeding. We found several *S. antillanca* walking on the prey, some of them around the host's mouth (Figs. 3–4). In those cases, although visibility was far from ideal, there was no evidence that the anapids were feeding from the fluids exposed by the chewing of the austrochiline. In another situation, where a host was feeding on a tipulid crane-fly, an in-



Figures 1–4.—*Sofanapis antillanca* on webs of austrochilines. 1, Female walking on host web, from Chepu; 2, Austrochiline and *S. antillanca* feeding on a tipulid, from Contulmo (arrow points to the anapid feeding on the tipulid's leg); 3, Austrochiline and *S. antillanca* feeding on a beetle, from Contulmo (arrows point to the four anapids); 4, Same, closer view.

dividual of *S. antillanca* was seen feeding directly from the insect's leg (Fig. 2). On another occasion, a specimen of *S. antillanca* was observed feeding alone on a small mosquito caught in an araneid web (also in the Parque Nacional Puyehue). This observation suggests that the anapid might have some ability to locate prey in the host's web, independent of the movements of the host, and that *S. antillanca* is not adapted to kleptoparasitism to the extreme condition of total depen-

dence on the host (as apparently occurs with *Curimagua bayano* Forster & Platnick 1977, a symphytognathid with reduced mouthparts, Vollrath 1978). Moreover, the presence of occasional individuals of *S. antillanca* on webs of araneids and hahniids (in the Monumento Natural Contulmo in Arauco, Region VIII, Chile), as well as in Berlese samples of leaf litter and moss, indicates that these spiders are not obligately associated with austrochilines. However, the particularly high density of *S.*

antillanca collected on austrochiline webs suggests a special association with these hosts.

Austrochilines are common in extremely to moderately moist forests of central and southern Chile and adjacent Argentina. However, the kleptoparasitic anapids were found only in the most humid localities. In addition to the Puyehue and Contulmo localities noted above, *Sofanapis* have been taken from austrochiline webs at the following localities in Chile: Calleta La Arena in Llanquihue, and 15 km S of Chepu in Chiloé (both in Region X). Several intense but fruitless searches were performed in less humid localities, in both Chile and Argentina.

Material examined.—(Most austrochilines were either juveniles or were not collected together with its kleptoparasites): **CHILE:** *Región IX:* Cautín, Monumento Natural Contulmo, elev. 340 m, 38°01'S, 73°11'W, 13 February 1992 (N. Platnick, P. Goloboff, M. Ramírez) 4♀ *S. antillanca* (Figs. 3, 4, AMNH); 18 November 1993 (N. Platnick, K. Catley, M. Ramírez, T. Allen) 1♂ *S. antillanca* (Fig. 2, AMNH). *Región X (Los Lagos):* Osorno, P. Nac. Puyehue, Aguas Calientes, 12 February 1992 (Platnick, Goloboff, Ramírez) many ♂♀ *S. antillanca* on a web of a female *Thaida peculiaris* Karsch (AMNH). Llanquihue, Caleta La Arena, 30 January 1991 (M. Ramírez) 2♂3♀ 2juv *S. antillanca* on a web of a subadult ♂ austrochiline (MACN); same data, 2♀ 1 juv on uncollected austrochiline's web. Chiloé, Chepu, 15 km S de Chepu, 3 February 1991

(M. Ramírez) 1♂6♀ 1juv, on uncollected austrochiline's web (Fig. 1, MACN).

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RESEARCH NOTE

CARBOHYDRATE ANALYSIS IN SPIDER HEMOLYMPH OF SELECTED LYCOSID AND ARANEID SPIDERS (ARANEAE: LYCOSIDAE AND ARANEIDAE)

The literature gives incomplete and conflicting information concerning the carbohydrate composition of hemolymph in the Araneae. Various analyses of hemolymph components have been reported on several spiders including: the spider *Cupiennius salei* (Keyserling 1877) by Loewe et al. (1970); the theraphosid *Aphonopelma hentzi* (Girard 1854) by Stewart & Martin (1970); the large orb weaver *Nephila madagascarensis* (Vinson 1863) by Rakatovao & Ratsimamanga (1975); the spider *Hexathele hochstetteri* Ausserer 1871 by Bedford (1977); the araneids *Araneus gemma* (McCook 1888) and *Argiope trifasciata* (Forskål 1775) by Cohen (1980); selected species of the family Lycosidae by Punzo (1982); sparassids, pisaurids, and amaurobids by Punzo (1983); the theraphosid *Eurypelma californicum* Ausserer 1871 by Schartau & Leidescher (1983); hemolymph inorganic ions in 15 spiders and six scorpion species by Burton (1984). Punzo (1989) studied four species of mygalomorphs *Bothriocyrtum californicum* (O.P. Cambridge 1874), *Aphonopelma echinum* (Chamberlin 1940), *Euagrus comstocki* Gertsch 1935, and *Atypus bicolor* Simon 1836.

With regard to the identity of carbohydrates present in the hemolymph, Rakatovao & Ratsimamanga (1975) and Bedford (1977) identified trehalose and glucose, while Schartau & Leidescher (1983) identified only glucose. Loewe et al. (1970) and Stewart & Martin (1970) hypothesized the presence of trehalose because their data indicated sugars other than glucose present. The studies by Cohen (1980) and Punzo (1982, 1983, 1989) quantified carbohydrate concentration differences among species but did not identify the carbohydrate(s) present. The studies by Loewe et al. (1970) and Schartau & Leidescher (1983) reported the presence of circulating glycopro-

teins, while the other studies did not test for these carbohydrates. The findings of Loewe et al. (1970), Stewart & Martin (1970), and Bedford (1977) indicate individual variation within conspecifics, while the other studies report total carbohydrate concentration within a given species.

In an attempt to clarify the carbohydrate composition of spider hemolymph, this study was conducted using *Argiope aurantia* Lucus 1833, *Hogna carolinensis* (Walckenaer 1805), *Arctosa littoralis* (Hentz 1844), and *Rabidosia rabida* (Walckenaer 1837). Spiders used in this study were collected in north-central Texas. Species were selected based on availability, size, and volume of hemolymph recovered from each individual. Voucher specimens of species used in the study are on deposit at the American Museum of Natural History (AMNH), New York. The lycosids were placed in metal cans (10 cm × 14 cm) which contained a small amount of soil, offered crickets and water, and were tested within 48 h of collection. Since *A. aurantia* is an orb weaver, the specimens were removed from the webs, brought to the laboratory, and tested. The spiders were anesthetized with carbon dioxide and placed on a surgical restraint following Randal (1980). The legs were severed at mid-femur and hemolymph was collected with capillary tubes, which were stored in 400 µl microfuge tubes. The tubes were labeled and centrifuged at 12,000 × g for 10–12 min. The resultant cell-free hemolymph was refrigerated at approximately 3 °C and analyzed within 72 h.

Assays included total anthrone reaction to carbohydrates in untreated hemolymph and anthrone reaction after protein precipitation (Dubois et al. 1956) and specific enzyme digestion with glucose oxidase (Fleming & Peggler 1963) with and without trehalase digestion.

A variation on the phenol-sulfuric acid test, using an addition of trichloroacetic acid (TCA) to bring the sample to a total of 5% TCA, was used to test for free carbohydrate. This new sample at 5% TCA was centrifuged 8–10 min at $12,000 \times g$, and 200 μ l of the resultant clear supernatant was retained for total carbohydrate analysis.

Solutions of known concentration were used to plot standard curves from the resultant absorbance data at 470 nm in order to quantify total carbohydrates. Each group of spider hemolymph was analyzed against standards prepared at the same time. There was a range of variation among individuals for total carbohydrate concentration. As an example, *R. rabida* exhibited a range from 3.54 μ g to 45.8 μ g of carbohydrates per 10 μ l of hemolymph. The variation in the amount of total carbohydrate present was a consistent feature of the data (C.V. = 44).

Total glucose was determined from comparisons of glucose oxidase activity of solutions of known concentration. Considerable individual variation occurred in the amount of glucose present in 5 μ l hemolymph samples. Absorbance data for each control group varied. With regard to different sets of individuals, the data were qualitatively based on variance of these standard absorbencies.

The amount of glucose present after digestion with trehalase was determined for *A. aurantia*. The total amount of glucose present increased following treatment of the hemolymph with trehalase. Based on a two point ANOVA, glucose present after trehalase digestion did not differ from the total amount of glucose present before treatment ($P > 0.2$). For example, *A. aurantia* hemolymph contained an average of $5.77 \pm 2.12 \mu$ g of glucose per 5 μ l hemolymph without trehalase treatment and an average of $7.89 \pm 3.11 \mu$ g glucose per 5 μ l hemolymph after trehalase treatment.

Total carbohydrate analysis after protein precipitation with TCA was performed on 16 *A. aurantia* and two *R. rabida*. The presence of TCA altered the color yield for the glucose standard solutions. Thus, standards were treated the same way as the hemolymph samples and analyzed simultaneously (TCA and control samples) to correct for this effect. In comparing the total carbohydrates with and without TCA treatment, there was a two-fold decrease in the amount of carbohydrates pre-

sent in all but one of the 18 specimens tested. Free carbohydrates accounted for less than 50% of the carbohydrates present in the majority of the samples.

In summary, glucose is the only detectable carbohydrate present in the hemolymph. The differences between total carbohydrate and total glucose are small and may be accounted for by the change in color yield of the standards from test to test. Thus, the absorbance data sets are not readily comparable due to the shift in relative color yield. The increase in the amount of glucose present after trehalase treatment is not significant. Data indicate a high degree of individual variation among individuals in the concentration of glucose in the hemolymph. These varying concentrations may reflect the physiological conditions of the animal and the environmental stresses that are placed upon it (Clarke 1979). The data support the observation noted by Loewe et al. (1970) and Schartau & Leidescher (1983) that glucose exists partially in glycoproteins. Free glucose accounts for less than 50% of the total glucose present in this study. More work is needed to describe the existence of a hemolymph glycoprotein in the Araneae. The extensive physiological work done on the class Insecta should serve as a model for investigations in other classes of arthropods.

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 33, 34, *A-us y-us*, male. Scale = 1.0 mm.

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Cover photo: A green lynx spider (*Peucetia viridens*) holding a wasp by the antennae. As the spider held the wasp, two more wasps arrived and attempted to mate with the wasp. (Photo by Gail Stratton)

REVISION AND CLADISTIC ANALYSIS OF THE ERIGONINE SPIDER GENUS *SISICOTTUS* (ARANEAE, LINYPHIIDAE, ERIGONINAE)

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ABSTRACT. The erigonine spider genus *Sisicottus* is revised for the first time. Cladistic analysis of *Sisicottus* suggests the following hypothesis of interspecific relationships: ((*S. montigenus*, *S. quoylei*) (*S. panopeus* (*S. montanus* (*S. crossoclavis* (*S. cynthiae* (*S. orites* (*S. nesides*, *S. aenigmaticus*)))))). The monophyly of the genus is unambiguously supported by six putative synapomorphies: a terminal embolic hook, a suprategular membrane projecting apically from the distal suprategular apophysis, copulatory ducts that originate on the ectal side of the spermathecae, imbricated stridulatory striae, the presence of two dorsal macrosetae on tibia III, and the absence of a trichobothrium on metatarsus IV. Evidence for the monophyly of each *Sisicottus* species is discussed. A taxonomic key, diagnoses, descriptions, quantitative character values, illustrations, locality records, natural history information, and distribution maps are presented for the nine recognized species. Five new species are described: *S. quoylei*, *S. panopeus*, *S. crossoclavis*, *S. cynthiae*, and *S. aenigmaticus*. *Typhochrestus uintanus* (NEW COMBINATION) is formally transferred out of *Sisicottus*.

The genus *Sisicottus* Bishop & Crosby 1938 (Linyphiidae) is a lineage of small to medium-size erigonine spiders made up of nine known species. *Sisicottus* species usually live in moss and litter in conifer forests where they presumably build small prey capture webs. The genus is known from North America north of Mexico and from the Kuril Islands between Japan and the Kamchatka Peninsula. It is most diverse in the northwestern United States and southwestern Canada.

By 1995, *Sisicottus* was one of 534 valid linyphiid genera (Platnick 1997). However, it is one of few linyphiid genera defined explicitly by putative synapomorphies. At best, most linyphiid genera seem to be delimited to preserve homogeneity among members. The quality of systematics as an information storage and retrieval system is undermined when genera are circumscribed without due consideration of evidence in support of monophyly. The original diagnosis of *Sisicottus* was inadequate to prevent *Sisicottus* from serving as a polyphyletic wastebasket. Species once placed in *Sisicottus* are currently placed in four different genera. The erroneous placement of some species in *Sisicottus* appears to

have been based on understandable misinterpretations of homology. In other cases, placement in *Sisicottus* seems inexplicable.

Some morphological features in *Sisicottus* exhibit a range of evolutionary plasticity. The distal suprategular apophysis of the male palpus is recognizably different in every *Sisicottus* species. The shape of the male palpal tibia and the dorsal plate of the female epigynum exhibit slightly less interspecific variation. Other characters, such as the form of the male paracymbium, the marginal suprategular apophysis of the palpus, the embolic division, and the path of the female copulatory ducts are nearly invariant within the genus. If one gives primacy to such characters, *Sisicottus* does in fact comprise a homogeneous group of species. But relying on intuition to predict which characters will be stable and which will be homoplastic is unscientific. Shared derived similarity (synapomorphy) is the evidence upon which monophyletic groups are recognized. Synapomorphies are best discovered by incorporating as much comparative data as possible into a cladistic analysis. The task of bringing phylogenetic order to the chaos that is linyphiid systematics is a monumental one,

but its reward will be a hierarchical structure based on repeatable methods and explicit character evidence. Currently, even most professional spider systematists can identify linyphiids only with difficulty or not at all. An active dialog on the comparative morphology of linyphiids and the history of character states will lead to a phylogenetically based and usable taxonomy. An improved taxonomy will facilitate the communication of ideas and findings concerning this diverse and important spider family. Such communication will not be limited to professional spider systematists, but will include ecologists, biogeographers, conservationists, and amateur taxonomists.

TAXONOMIC HISTORY

Bishop & Crosby (1938) established *Sisicottus* to accommodate *Tmeticus montanus* Emerton 1882 and a new species, *Sisicottus montigenus* Bishop & Crosby 1938. They diagnosed the genus based on characteristics of the male palpus. According to the original description, the two founding species shared similar dorsomesal tibial apophyses, a lamella characteristica (misidentified as a radical tail-piece) described as "bulb-like," and an open-coiled embolus making one turn about the distal end of the bulb (Bishop & Crosby 1938: 57).

Bishop & Crosby synonymized *Erigone collina* Marx 1890, *Grammonota orites* Chamberlin 1919, *Oedothorax nesides* Chamberlin 1921, and *Oedothorax pidacitis* Crosby & Bishop 1927 under *S. montanus*. Although Bishop & Crosby recognized that a "larger and usually somewhat paler" (Bishop & Crosby 1938:59) form existed sympatrically in the west with the smaller form of *S. montanus* typical of eastern populations, they were unable to come up with a reliable way of separating the two morphs. The western form aluded to is undoubtedly *S. orites* and/or *S. nesides*. Both of these species are common and widespread in the west and are larger than *S. montanus*. However, the observation that these western species are typically paler than *S. montanus* is erroneous.

Working near the end of the 19th century, Marx objected to the trend begun by his contemporaries Menge, Emerton, and Simon, of splitting *Erigone* Audouin 1826 into the many smaller genera that now comprise the Erigoninae. Instead of transferring previously de-

scribed species into *Erigone*, Marx's (1890) catalog features several replacement names for valid species. One example of this was *E. collina*, which was meant to replace *T. montanus*.

Chamberlin & Ivie (1933) synonymized *Oedothorax pidacitis* under *Grammonota orites* and transferred the species to *Oedothorax* Bertkau 1883, making it congeneric with the very similar *O. nesides*. Shortly after the establishment of *Sisicottus* as a new genus, Chamberlin & Ivie (1939) rejected the broad definition of *S. montanus* and re-elevated *S. orites* and *S. nesides* to species status. Although they wrote no justification for their decision, they did illustrate the dorsal view of the male palpal tibiae of *S. orites*, *S. nesides*, and *S. montanus*. Chamberlin & Ivie also placed two new species in *Sisicottus*: *S. uintanus* Chamberlin & Ivie 1939 and *S. cornuella* Chamberlin & Ivie 1939.

Holm (1967) suggested that *S. uintanus* be transferred to *Typhochrestus* Simon 1884 based on a comparison with *T. pygmaeus* (Sørensen 1898), which is not the type species of the genus. He commented on the superficial similarity of an embolus coiled around a straight apophysis shared by *S. uintanus*, *S. montanus*, and *T. pygmaeus*, but realized that the apophysis of *S. uintanus* and *T. pygmaeus* arises from the embolic division whereas the apophysis in *Sisicottus* arises from the supratregulum or "median apophysis" in Holm's terminology. Although this change has been adopted by some authors (Buckle et al. 1994), Holm's statement was too tentative to meet Platnick's (1989) criteria for formal transfers.

Sisicottus cornuella was transferred to *Walckenaeria* Blackwall 1833 by Millidge (1983) apparently based on characteristics given in his definition of *Walckenaeria* (e.g., sternum longer than wide, distinctly sclerotized pedicel, fourth metatarsal trichobothrium, strongly pectinate tarsal claws) and on the presence of a short horn on the male carapace and details of the male and female genitalia typical of the *minuta* group of *Walckenaeria* species.

Sisicottus atypicus Chamberlin & Ivie 1944 was described from the male only. *Sciastes ogeechee* Chamberlin & Ivie 1944 was described from a single female in the same paper. These two species were later found to be conspecific and were synonymized under *Souessoula parva* (Banks 1899) by Ivie

(1967). This species lacks nearly all of the characteristics that distinguish *Sisicottus* from other erigonines including a coiled embolus.

Sisicottus hibernus Barrows 1945 is a very unusual species that was inexplicably described as a *Sisicottus*. It shares none of the synapomorphies that define *Sisicottus* and was transferred to *Carorita* Duffey & Merrett 1963 by Zujko-Miller (1999) based on the results of a phylogenetic study.

METHODS

Abbreviations for anatomical structures and quantitative characters are listed in Table 1. Abbreviations for specimen collections are found in the acknowledgments. Boundaries for quantitative characters are illustrated in Figs. 1, 2, 5–7, and 22–24. All measurements are in mm.

Light microscopy.—Measurements were performed using a Leitz binocular dissecting scope with greenough objectives and an eyepiece micrometer scale in 20× oculars. Five specimens were remeasured five times for each character during this study. This sampling indicated that the measurements are accurate to one micrometer unit for both powers of magnification used. Carapace length was measured at 80× and one micrometer unit had a value of 0.024 mm. All other measurements were made at 200× and one micrometer unit had a value of 0.0095 mm. Illustrations of external structures were drawn using a 20 × 20 ocular grid at 200×. For observation of internal structures, specimens were cleared in methyl salicylate (Holm 1979) and illustrated using an Olympus BH-2 compound microscope at 400× fitted with a camera lucida. Cleared specimens were positioned for illustration using the method described by Coddington (1983). Male palpus drawings and scanning electron micrographs are from the left appendage unless otherwise indicated. Specimens in which tracheal structures were to be viewed had windows cut in the dorsal integument of the carapace and abdomen. Specimens were digested in dilute sodium hypochlorite (household bleach) at room temperature for several hours until all the non-chitinous parts had dissolved (Millidge 1984a). Chlorazol black was used to stain the tracheae. Illustrations were made using a Wild M-20 compound microscope fitted with a camera lucida.

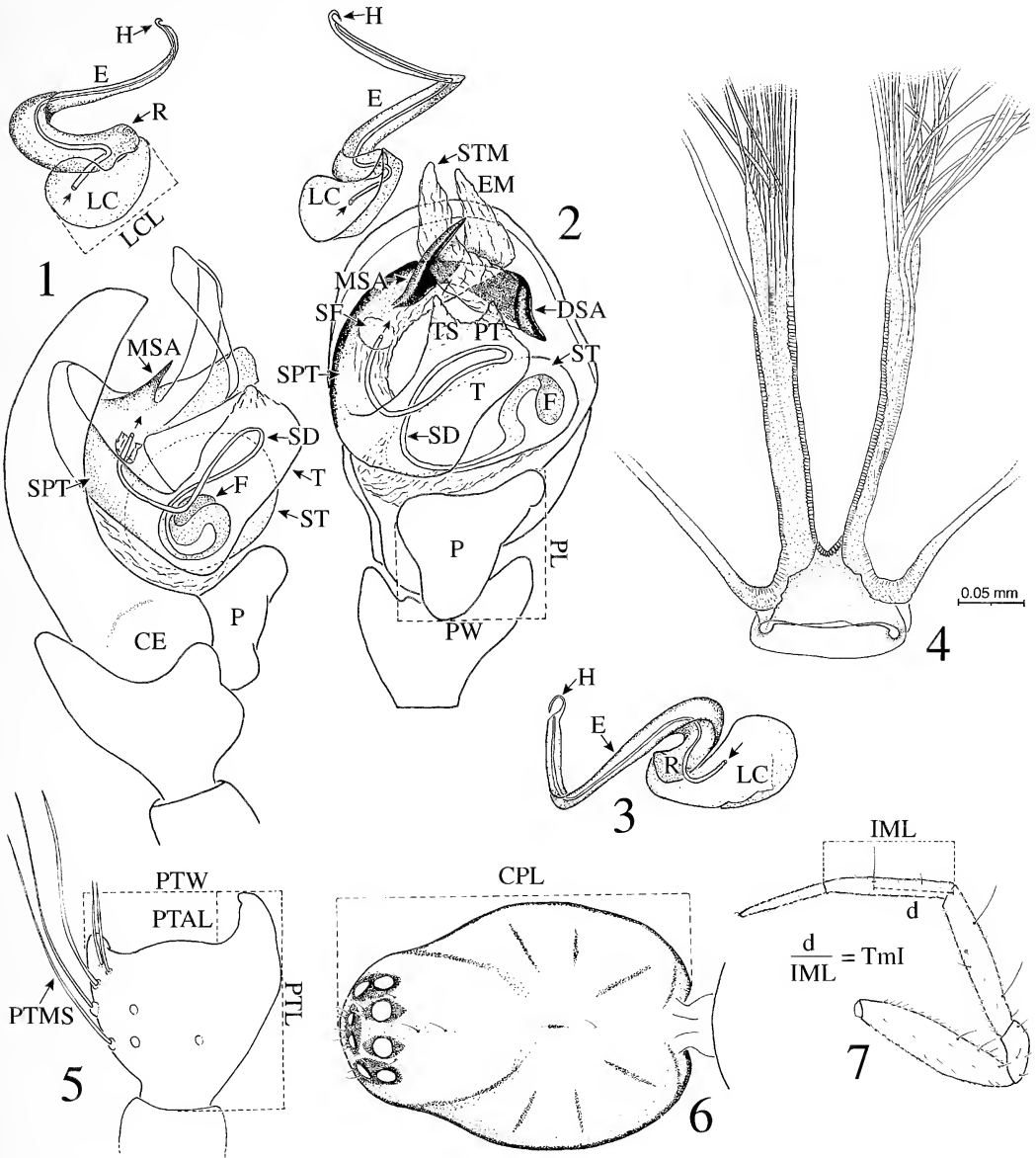
Electron microscopy.—Scanning electron microscopy (SEM) was conducted using a Jeol 35U at Clemson University and an Am-ray 1810 at the National Museum of Natural History (Smithsonian Institution). Male and female specimens representing most *Sisicottus* species were examined using SEM. I was unable to examine *Sisicottus aenigmaticus* new species or males of *S. quoylei* new species. Male and female specimens of *Typhochrestus uintanus* and *T. digitatus* (O. Pickard-Cambridge 1872) were also examined. This last species was represented by specimens prepared by G. Hormiga according to methods described in Hormiga (in press). I used SEM to observe male and female genitalia and spinneret spigot morphology. Spinneret spigots were identified using Coddington (1989). Abdomens and some genitalia were prepared for SEM by taking them through a rehydration series, placing them in a buffered 2.5% glutaraldehyde solution for 48 hours, then dehydrating to 100% ethanol. Specimens were then ultrasonicated for up to one minute. Ethanol was then removed either by critical point drying in a Seevac CPD-100 or preparation in hexamethyldisilazane for five minutes (Polysciences, Inc., CAT #0629). Some genitalia were simply ultrasonicated, dehydrated in 100% ethanol, placed in hexamethyldisilazane, air dried, and mounted.

Quantitative characters.—Quantitative characters were selected on the basis of their estimated potential utility in distinguishing species and groups of species. Quantitative character values for samples of each species (Tables 2, 3) and for the type specimens alone (Table 4) are an important part of each description.

Descriptions.—Species descriptions draw from as many individuals over as wide a geographic range as possible. This approach was chosen in order to account for as much intra-specific variation as possible. Some illustrations required the examination of multiple specimens to achieve a clear interpretation of the anatomy. Because of the relative difficulty involved in distinguishing some species, the diagnostic section of each species description has been designed to convey all available information that might be relevant to accurate species identification. Descriptions highlight the unique characteristics of each species and

Table 1.—Anatomical and quantitative abbreviations used in text, figures, and tables. For morphometric characters, maximum lengths were recorded unless otherwise specified, # indicates a quantitative character.

AC	aciniform gland spigot(s)	mAP	minor ampullate spigot(s)
AG	aggregate gland spigot(s)	MSA	marginal supratégular apophysis (♂)
ALS	anterior lateral spinneret(s)	NU	nubbin
ARP	anterior radical process (♂)	P	paracymbium (♂)
CD	copulatory duct (♀)	PI	piriform gland spigot(s)
CDC	copulatory duct capsule; sclerotized capsule which covers the copulatory ducts (♀)	PL	paracymbium length, ventral view (♂, #)
CDCW	copulatory duct capsule width, dorsal view (♀, #)	PLS	posterior lateral spinneret(s)
CE	excavation of cymbium on mesal side (♂)	PME	posterior median eyes
CO	copulatory opening (♀)	PMS	posterior median spinneret(s)
CPL	carapace length, dorsal view (#)	PT	protegulum (♂)
CY	cylindrical gland spigot(s)	PTL	palpal tibia length (♂, #)
DF	dorsal fold of dorsal plate (♀)	PTA	palpal tibial apophysis (♂)
DP	dorsal plate of epigynum (♀)	PTAL	palpal tibial apophysis length measured from concavity between dorsomesal apophysis and ectal tibial process (♂, #)
DPP	sclerotized posterior face of dorsal plate (♀)	PTMS	number of macrosetae in ectal cluster on palpal tibia (♂, #)
DPPH	dorsal plate, posterior face height (♀, #)	PTW	palpal tibia width (♂, #)
DPPW	dorsal plate, posterior face width (♀, #)	PW	paracymbium width, ventral view (♂, #)
DSA	distal supratégular apophysis (♂)	R	radix (♂)
E	embolus (♂)	S	spermatheca (♀)
EF	epigastric furrow (♀)	SD	sperm duct (♂)
EL	length of epigynum from anterior margin of copulatory duct capsule to posterior margin of dorsal plate, dorsal view (♀, #)	SF	supratégular foramen (♂)
EM	embolic membrane (♂)	SPT	supratégulum (♂)
ETP	ectal tibial process (♂)	ST	subtegulum (♂)
F	fundus or reservoir (♂)	STM	supratégular membrane (♂)
FD	fertilization duct (♀)	T	tegulum (♂)
G	groove in ventral plate (♀)	Tml	position of trichobothrium on metatarsus I (#)
H	hook on tip of embolus (♂)	TP	radical tail piece (♂)
IML	metatarsus I length (#)	TS	tegular sac (♂)
LC	lamella characteristic (♂)	VP	ventral plate of epigynum (♀)
LCL	length of lamella characteristic (♂, #)	VPID	ventral plate invagination depth (♀, #)
MAP	major ampullate spigot(s)	VPIW	ventral plate invagination width, minimum (♀, #)



Figures 1–7.—Morphology of *Sisicottus* with limits of some quantitative characters. 1, 2, Schematic illustrations of *Sisicottus* palpus. 1, Mesal view with embolic division detached; 2, Ventral view with embolic division detached; 3, Embolic division, ectal view; 4, Tracheal system of female *Sisicottus montanus* from Mt. Mansfield, Vermont, ventral view; 5, Male palpal tibia, dorsal view; 6, Female carapace, dorsal view; 7, Female left leg I, retrolateral view.

the particular expression of characters found across all *Sisicottus* species.

CLADISTIC ANALYSIS

Outgroup selection.—The Linyphiidae represent the largest family of web-building spiders in terms of species diversity (Coddington & Levi 1991). However, phylogenetic

relationships among linyphiids are poorly understood, especially among the largest subfamily, the Erigoninae (Hormiga 1993, 1994a, 1994b, in press). This state of almost complete phylogenetic ignorance complicated the problem of identifying close relatives for use as outgroups in the cladistic analysis of *Sisicottus*. *Sisicottus* was appended to a cladistic

analysis of erigonine phylogeny in Hormiga (in press). Outgroup taxa were selected based on the results of this reanalysis.

Hormiga's (in press) cladistic analysis of linyphiid spiders provides the most rigorous hypothesis so far of erigonine relationships. It incorporates 43 terminal taxa, including 31 erigonine genera, representing a wide cross section of the morphological diversity found among these spiders, scored for 73 characters. I reanalyzed Hormiga's data matrix after incorporating *Sisicottus*. All *Sisicottus* species are coded identically when incorporated into Hormiga's data matrix so a single exemplar was used to represent the genus. *Sisicottus* was coded as follows: 0001310101 1011110101 0?01001101 000?000101 0000000000 1000120111 0001100101 1?? (See Hormiga (in press) for character states and descriptions).

Nine exemplar taxa were taken from Hormiga's (in press) analysis to compose the outgroup: *Islandiana princeps* Brændegaard 1932, *Diplocentria bidentata* (Emerton 1882), *Typhochrestus digitatus* (O. Pickard-Cambridge 1872), *Erigone psychrophila* Thorell 1871, *Tmeticus tolli* (Kulczyński 1916), *Walckenaeria directa* (O. Pickard-Cambridge 1874), *Gonatium rubens* (Blackwall 1833), *Gongylidium rufipes* (Sundevall 1829), and *Oedothorax gibbosus* (Blackwall 1841). In addition, *Typhochrestus uintanus* (Chamberlin & Ivie 1939) was included to test Holm's (1967) suggestion that *Sisicottus uintanus* should be transferred to *Typhochrestus*. Character states for these taxa were evaluated using the following material: *I. princeps* [GREENLAND: Narssarsuaq, 61°10'N, 45°25'W, 5 July 1983, 1♂, (P. Nielsen, ZMUC); Western Greenland, Disko, Lyngmarksfjeld, 250 m, 13 July 1962, 1♀, (Å. Holm, ZMUC)], *D. bidentata* [RUSSIA: N.E. Siberia, Magadan area, Ola, 15–18 July 1992, 2♂16♀, (Y.M. Marusik, USNM). UNITED STATES: New York: Mount Whiteface, summit, 44°22'N, 73°55'W, 23 October 1936, 4♂10♀, (H. Dietrich, USNM); Mount Whiteface, 23 October 1936, 2♂2♀, (H. Dietrich, USNM). Utah: Smith and Morehouse Canyon, 40°47'N, 111°6'W, 7 October 1932, 3♂3♀, (W. Ivie, USNM).], *T. digitatus* [ENGLAND: Whiteford Burrows: 1 September 1965, 3♂6♀ (J.A.L. Cook, AMNH); 26 September 1966, 3♂1♀ (J.A.L. Cook, AMNH).], *T. uintanus* [UNITED STATES: Utah: Fish

Lake, 38°33'N, 111°43'W, 4 September 1929, 4♂4♀ (Chamberlin & Gertsch, AMNH); Mirror Lake, Uintah Mountains, 40°43'N, 111°53'W, 28 July 1936, 3♂1♀ (Ivie, AMNH)], *E. psychrophila* [UNITED STATES: Alaska: Point Barrow, 71°22'N, 156°30'W, 23 June 1963, 5♂3♀ (R.F. Ashley, AMNH)], *T. tolli* [RUSSIA: NE Siberia, Lankovava River (Ola River basin), 65°45'N, 152°N, 13–19 August 1992, 6♂17♀ (Y.M. Marusik, USNM)], *W. directa* [CANADA: British Columbia: Terrace, 54°31'N, 128°32'W, March 1933, 3♂1♀ (Hippisley, AMNH)], *Gonatium rubens* [ENGLAND: Surrey: Yorkshire, 2♂3♀ (Murphy, AMNH)], *Gongylidium rufipes* [ENGLAND: Oxford: Bampton and/or The Weald, 6 July 1965, 1♂1♀ (J.A.L. Cook, AMNH)], and *O. gibbosus* [ENGLAND: Fife: Tentsmuir Dune, 20 June 1966, 4♂14♀ (J.A.L. Cook, AMNH)]. Further analysis was conducted using *Hylyphantes graminicola* (Sundevall 1829) [ENGLAND: Surrey, 1♂2♀ (Murphy, AMNH)].

Characters.—The data matrix used to investigate relationships among *Sisicottus* species contained 41 phylogenetically informative characters. Eighteen concern the male palpus, 16 concern female genitalia, and seven concern somatic morphology. Eighteen characters (1, 6–10, 12, 13, 18, 28, 33, and 35–41) were taken or modified from Hormiga (in press). These are all of the characters in Hormiga's analysis that are phylogenetically informative with respect to relationships among the outgroup taxa and *Sisicottus*. All seven multistate characters (3, 8, 19, 21, 30, 31, and 38) were treated as unordered. Characters with ambiguous optimization were resolved to favor secondary loss over convergence (Farris or ACCTRAN optimization) unless otherwise stated. An expanded treatment of each character used in the analysis follows.

Male palpus: (1). Embolus length: 0 = short; 1 = long (Fig. 3, E). (2). Terminal embolic hook: 0 = absent; 1 = present (Figs. 3, 8, H). All species of *Sisicottus* have a hook on the terminal part of the embolus that curves back over the opening of the sperm duct. (3). Distal supratregular apophysis sclerotization: 0 = membranous; 1 = light; 2 = heavy. The distal supratregular apophysis is an extension of the supratregulum beyond the supratregular foramen, the aperture through which the sperm duct leaves the tegular divi-

sion (Hormiga in press). The distal suprategular apophysis of *Sisicottus montigenus* is generally transparent throughout its length. The distal suprategular apophysis of some other *Sisicottus* species is black and completely opaque. The intermediate state is usually orange in color and opaque to slightly translucent. (4). Distal suprategular apophysis length: 0 = short (Fig. 61, DSA); 1 = long (Fig. 19, DSA). The short distal suprategular apophysis never extends more than about half way down the unexpanded palpal bulb. The long distal suprategular apophysis extends to about the ventral midline of the unexpanded palpal bulb. (5). Suprategular embolic membrane: 0 = absent; 1 = present (Figs. 2, 42, STM). This membrane arises from the distal suprategular apophysis. In *Sisicottus*, this membrane projects anteriorly and is closely associated with the embolic membrane and the tip of the embolus. (6). Marginal suprategular apophysis: 0 = absent; 1 = present (Figs. 2, 42, MSA). The marginal suprategular apophysis is a tooth-like process on the distal part of the suprategulum and is located near the suprategular foramen (Hormiga in press). The marginal suprategular apophysis of *Sisicottus* is straight and quite prominent. (7). Radical tailpiece: 0 = present; 1 = absent. (8). Shape of radical tailpiece: 0 = straight; 1 = spiraled; 2 = curved ectally; 3 = anteriorly directed. The radix is the sclerite of the linyphiid palpus through which the sperm duct passes between the column and the embolus. In addition, the radix may have a process known as the tailpiece that is highly variable in form across taxa. Homology between the araneid radix and the linyphiid radix has been seriously questioned on several occasions (Hormiga 1993, 1994a). Recent phylogenetic analyses of araneoid relationships have concluded that araneids and linyphiids are somewhat distantly related and the presence of a radix can only be optimized as evolving independently in araneids and linyphiids (Hormiga et al. 1995; Scharff & Coddington 1997; Griswold et al. 1998). Close relatives of linyphiids include pimoids, theridiids, theridiosomatids, and tetragnathids, none of which have a sclerite that can be convincingly homologized with the linyphiid radix (Coddington 1990; Hormiga 1994b; Hormiga et al. 1995). The status of the linyphiid radix as a synapomorphy for the Linyphiidae seems well

supported by the data available (Hormiga in press). (9). Lamella characteristica: 0 = absent; 1 = present (Fig. 59, LC). The lamella characteristica arises from the basal part of the radix and does not conduct the sperm duct (Hormiga 1994a). Some erigonines have both a radical tailpiece and a lamella characteristica (e.g., *Gonatium rubens*, fig. 10f, Hormiga in press). (10). Anterior radical process (process of radical part (rpp) *sensu* Merrett 1963): 0 = absent; 1 = present. The anterior radical process arises adjacent to the embolus and projects distally (Hormiga in press). (11). Shape of anterior radical process: 0 = short; 1 = long, spiral (Figs. 111–113, ARP). A long, spiraled anterior radical process is diagnostic for *Typhochrestus*. (12). Protegular papillae: 0 = absent; 1 = present. Protegular papillae are small and scale like in *Sisicottus* (Fig. 46); they are much more conspicuous in some other erigonines. (13). Tegular sac: 0 = absent; 1 = present (Fig. 2, TS). The tegular sac is a membranous process arising from the tegulum adjacent to the protegulum (Hormiga in press). (14). Paracymbium in ventral view: 0 = restricted to ectal side of palpus; 1 = a broad, flat plate that extends to the mesal side of the palpus (Fig. 2, P). (15). Cymbial excavation: 0 = small; 1 = conspicuous (Fig. 17, CE). All erigonines examined have a glabrous region on the mesal side of the cymbium near its junction with the palpal tibia. In *Sisicottus* and some other taxa, this region is quite conspicuous. In other taxa, this region is more or less restricted to the cymbial margin and often obscured by the palpal tibia. (16). Length of palpal tibial apophysis: 0 = short, hardly extending away from cymbium (Fig. 20, PTA); 1 = long, extending upward or anteriorly over cymbium (Fig. 94, PTA). (17). Ectal tibial process: 0 = strong (Fig. 94, ETP); 1 = weak or absent (Fig. 41). Many erigonines have a prominent, often ectally curving palpal tibial apophysis originating from the dorsomesal side of the tibia. The ectal tibial process is a smaller structure located on the dorsoectal side of the tibia. (18). Male pedipalpal patella ventral apophysis: 0 = absent; 1 = present.

Female genitalia: (19). Ventral plate: 0 = posterior margin overhangs epigastric furrow (fig. 156, Millidge 1984b); 1 = slightly invaginated (Fig. 43, VP); 2 = ventral plate deeply invaginated (Fig. 96, VP). (20). Me-

dian part of posterior margin of ventral plate in ventral view: 0 = distinctly convex (Fig. 110, VP); 1 = nearly flat to concave (Fig. 22, VP). (21). Posterior face of dorsal plate: 0 = subrectangular (Fig. 23, DPP); 1 = triangular with ventral apex (Fig. 63, DPP); 2 = triangular with dorsal apex; 3 = trapezoidal (Fig. 107, DPP). (22). Sides of posterior face of dorsal plate: 0 = nearly straight to convex (Fig. 23, DPP); 1 = distinctly concave (Fig. 107, DPP). (23). Ventral margin of posterior face of dorsal plate: 0 = distinctly concave (fig. 149, Millidge 1984b); 1 = nearly straight to convex (Figs. 23, 64, DPP). (24). Dorsal fold of dorsal plate: 0 = membranous (Fig. 24, DF); 1 = sclerotized (Fig. 71, DF). In dorsal view, a fold on the posterior margin of the dorsal plate forms a surface that may be membranous or sclerotized. (25). Copulatory openings: 0 = small; 1 = large and conspicuous (Fig. 110, CO). (26). Copulatory duct origin: 0 = ectal (Fig. 24, CD); 1 = mesal (fig. 603, Wiehle 1960). Copulatory ducts may originate from either the ectal or mesal side of the spermathecae. (27). Copulatory duct path: 0 = without distinct anterior projection (fig. 160, Millidge 1984b); 1 = with distinct anterior projection (Fig. 24, CD). (28). Copulatory duct encapsulation (Millidge 1984a): 0 = absent; 1 = present (Fig. 65, CDC). (29). Copulatory duct capsule: 0 = partial (fig. 21f, Hormiga in press); 1 = complete (Fig. 65). The copulatory duct capsule arises from the spermathecae and partially covers the copulatory ducts. In some cases, the capsules from each spermatheca meet in the center and may fuse together. This is a complete capsule. When not joined centrally, the capsule is partial. (30). Lateral lobes at anterior margin of complete capsule: 0 = concave (Wiehle 1960, fig. 603); 1 = straight (Fig. 38, CDC); 2 = convex (Fig. 65, CDC). In dorsal view, the epigynal capsule of *Sisicottus* species is roughly m-shaped with the two arches of the "m" oriented anteriorly. The lateral lobes at the anterior margin of the capsule are analogous to the humps on either side of the top of the "m." In all *Sisicottus* species, this region is straight or with a pair of convex lobes. (31). Lateral margin of complete capsule: 0 = simple curve to sinuous (Fig. 65, CDC); 1 = strongly bowed (Fig. 98, CDC). In some species, the legs of the "m" on the right and left side form strongly bowed convex lateral mar-

gins. All species with this character state have the left and right feet of the "m" oriented mesally toward each other. (32). Orientation of posterior part of complete capsule: 0 = posterior (Fig. 65, CDC); 1 = mesal (Fig. 78, CDC). The left and right feet of the "m" may be oriented mesally toward each other even if the capsule is not strongly bowed. (33). Fertilization duct orientation on exit from spermathecae: 0 = posterior (Millidge 1984b, fig. 160); 1 = mesal (Fig. 33, FD). (34). Fertilization duct shape: 0 = straight to sinuous (Fig. 24, FD); 1 = spiral (Fig. 98, FD).

Somatic morphology: (35). Male cephalic region: 0 = not raised; 1 = raised. (36). Male post-PME lobe: 0 = absent; 1 = present. (37). Male cephalic cuticular pores: 0 = absent; 1 = present. (38). Cheliceral stridulatory striae: 0 = ridged; 1 = scaly; 2 = imbricated (Fig. 10). (39). Dorsal spur on male chelicera: 0 = absent; 1 = present. (40). Dorsal macrosetae on tibia III: 0 = two; 1 = one. (41). Trichobothrium on metatarsus IV: 0 = absent; 1 = present. All characters of the somatic morphology considered in this analysis are constant within *Sisicottus*. See Hormiga (in press) for further discussion of these characters.

Analysis.—I used Hennig86 version 1.5 (Farris 1988), PAUP version 3.1.1 (Swofford 1993), and NONA version 1.6 (Goloboff 1993a) to analyze Hormiga's (in press) data matrix with *Sisicottus* appended (44 taxa, 73 characters). I then used these same programs and search strategies to analyze the data matrix in Table 5 for the most parsimonious phylogenetic hypothesis of *Sisicottus* species. Further analysis of *Sisicottus* species relationships was conducted using Pee-Wee version 2.6 (Goloboff 1993b) to calculate the fittest tree (Goloboff 1993c) and PHAST version 1.1 (Goloboff 1995) to calculate the Bremer support index (Bremer 1988).

In Hennig86, I used the "mh*,bb*" search strategy. In PAUP, I ran a heuristic search with 100 replicates of random taxon addition subjected to tree bisection-reconnection branch swapping. In NONA, I ran a search with the "mult*" random taxon addition algorithm for 100 replicates followed by the "max*" branch-swapping algorithm. This strategy was repeated under both the "amb=" (modified rule 3) and "amb-" (rule 1) settings. Hennig86 and PAUP use only rule 3. Under rule 1, branches are collapsed if the minimum pos-

sible branch length is zero, i.e., if all characters with potential support for a node can be placed on other branches. Under rule 3, branches are collapsed only if the maximum possible branch length is zero, i.e., if there is no character that can be optimized to support a node. Under the “amb=” setting, nodes are also collapsed if the ancestral and descendant state sets are identical. This version of rule 3 is slightly different from that implemented in Hennig86 and PAUP (see also Coddington & Scharff 1994).

Successive character weighting (Farris 1969; Carpenter 1988) by the maximum value of the rescaled consistency index was performed in PAUP with the base weight set to 1000. Trees found by Hennig86, PAUP and NONA (under the “amb=” setting) were imported into PAUP. NONA trees were saved using the ksv* command. PAUP will arbitrarily resolve polytomies in trees saved using NONA's sv command. The solution set from all three programs (Hennig86, PAUP, and NONA) was combined. Duplicate trees were eliminated. The remaining unique trees were then filtered to exclude polytomous trees when more highly resolved compatible trees were found (Coddington & Scharff 1996). This set of trees was reweighted and the data reanalyzed in PAUP.

For the analysis of *Sisicottus* species, I calculated the fittest tree in Pee-Wee using the “mult*100” command followed by the “max*” algorithm under the “amb=” setting. I used the entire range of values for the concave function allowed by Pee-Wee (“conc1” through “conc6”). This setting determines the shape of the concave function of homoplasy used to calculate fit. Lower values of the concave function deviate more extremely from the linear function of homoplasy that is equivalent to standard parsimony (Goloboff 1993b, 1993c). I calculated the Bremer support index (Bremer 1988) using PHAST with the following commands: “h*”, “amb-”, “sub5”, “find*”, “bs”. I used MacClade version 3.0 (Maddison & Maddison 1992) to analyze character optimization.

RESULTS

Phylogenetic context.—The cladistic analysis of Hormiga's (in press) data matrix plus *Sisicottus* yielded multiple most parsimonious rule 3 trees. Hennig86 found 12 trees while

PAUP and NONA each found 18 trees. NONA also found two rule 1 trees. Both of the rule 1 trees are less resolved than any of the trees found under rule 3. After the exclusion of six uninformative characters, all 20 trees had a length of 225 steps, a consistency index of 0.378 and a retention index of 0.680. One of the rule 3 trees is identical to Hormiga's (in press) preferred topology with *Sisicottus* placed sister to *Oedothorax*. A strict consensus of all rule 3 trees, all rule 1 trees, or all trees from both sets is identical. The consensus tree places *Sisicottus* in a polytomy with *Oedothorax*, *Hylyphantes* Simon 1884, and *Gongylidium* Menge 1868. Among the alternative most parsimonious trees, *Sisicottus* is either placed sister to *Oedothorax* or to a clade consisting of *Oedothorax*, *Hylyphantes* and *Gongylidium*. In the consensus tree, the four taxon clade containing *Sisicottus* is part of another polytomy consisting of *Walckenaeria*, *Gonatium*, and a resolved clade made up of *Grammonota* and six other genera. *Tmetiscus* and *Erigone* have a pectinate arrangement out from this polytomy. Sister to all other “distal erigonines” is a clade composed basally of *Islandiana* and *Diplocentria*. Five other genera are also included in this clade including *Typhochrestus*. There are two additional areas of conflict: relationships among *Drepanotylus*, *Sciastes*, and the “distal erigonines” clade, and also relationships among the linyphiines, the micronetines, and all other linyphiids. Both of these areas of conflict were present in Hormiga's (in press) original analysis.

Among the rule 3 trees found by Hennig86, PAUP and NONA, only six were both unique and more resolved than otherwise compatible trees. Successive character weighting of these six trees results stabilizes on a different set of six trees. This result is stable to subsequent iterations of reweighting. The strict consensus of the six reweighted trees is consistent with Hormiga's (in press) preferred topology. Relationships among the “distal erigonines” are identical and fully resolved in all six trees. The “distal erigonines” are topologically identical to Hormiga's (in press) preferred tree with *Sisicottus* placed sister to *Oedothorax*.

Phylogeny of *Sisicottus*.—The analysis of the data matrix in Table 5 yielded three most parsimonious trees. Results were identical under both rule 1 and rule 3 analyses. Each tree

had a length of 101 steps, a consistency index of 0.485, and a retention index of 0.681. Relationships among *Sisicottus* species were identical in all three trees. In the outgroup, the three possible resolutions of *Gonatium*, *Gongylidium*, and the *Oedothorax* plus *Sisicottus* clade make up the three most parsimonious trees. Otherwise, outgroup relationships are identical to the topology in Hormiga (in press). All most parsimonious trees support the monophyly of *Typhochrestus*.

Successive character weighting of the three most parsimonious trees stabilizes on a single tree (Fig. 115). This tree is identical to one of the most parsimonious tree under equal weights. Outgroup relationships are identical to those preferred by Hormiga (in press). Pee-Wee's implied weights algorithm found the topology in Fig. 115 when the concavity function was set between 4 and 6. For lower values of the concavity function, outgroup relationships were rearranged. These topologies found *Gongylidium* to be the sister taxon to *Sisicottus* and added one or two extra steps under equal weights. In all Pee-Wee trees, relationships among *Sisicottus* species were identical.

Although Hormiga's (in press) hypothesis of erigonine relationships is a great step forward in linyphiid systematics, several nodes are somewhat weakly supported by the available data. This is evidenced by the sensitivity of the topology to taxon sampling. According to the modified version of Hormiga's analysis, *Hylyphantes* is sister to the *Gongylidium*-*Oedothorax*-*Sisicottus* clade. However, inclusion of *Hylyphantes graminicola* (Sundevall 1829) in the analysis of *Sisicottus* resulted in six trees, none of which are consistent with Hormiga's (in press) topology. Nevertheless, relationships among *Sisicottus* species were the same in all trees and identical to those shown in Fig. 115. All trees support the monophyly of *Typhochrestus*. *Hylyphantes* can be added to Table 5 as follows: 0010001-10-101110121 001000110- -010000111 1.

Optimization and support.—Six unambiguous synapomorphies support the monophyly of *Sisicottus* (node 8): a terminal embolic hook (character 2), a suprategular membrane projecting apically from the distal suprategular apophysis (character 5), copulatory ducts that originate on the ectal side of the spermathecae (character 26), imbricated

stridulatory striae (character 38), the presence of two dorsal macrosetae on tibia III (character 40), and the absence of a trichobothrium on metatarsus IV (character 41). The loss of the ectal tibial process (character 17) and the absence of a dorsal spur on the male chelicera (character 39) are also optimized to support this node under Farris optimization. The Bremer support index (Bremer 1988) gives node 8 five steps of support making it the best supported node in the analysis. Additional character optimizations and Bremer support values are illustrated in Fig. 115.

Exceptions to Farris optimization were made for characters 12 (protegular papillae), 30 (shape of lateral lobes at anterior margin of complete capsule), and 37 (male cephalic cuticular pores). Character 12 must be optimized either at node 9 or 10. Farris optimization would place a change in character 12 at node 9. However, since *Gongylidium rufipes* lacks a protegulum, it was coded as not applicable for character 12. Optimizing character 12 at node 9 implies a hypothesis of synapomorphy where data are available for only one of the sister clades. Only at node 10 is there evidence of synapomorphy. The case with character 30 is very similar to that of character 12 with a step required at either node 12 or 13 for a character that is not applicable for *Tmeticus tolli*. Character 37 was optimized as an autapomorphy of *Typhochrestus digitatus* rather than a synapomorphy of clade 15. The character state of *T. uintanus* was not determined for character 37. This optimization maintains a conservative estimate of the character support for a monophyletic *Typhochrestus* recircumscribed to include *T. uintanus*. The monophyly of *Typhochrestus* (node 15) is unambiguously supported by 5 characters.

Character 28 (copulatory duct encapsulation) equivocally satisfies Farris optimization criteria under both possible resolutions. Hormiga's (in press) analysis indicates that the primitive condition for node 18 in Fig. 115 is the presence of copulatory duct encapsulation. Character 28 has been optimized to reflect this hypothesis.

The presence of a paracymbium that is wide in ventral view (character 14) is a rare character state among erigonines that is useful in diagnosing *Sisicottus*. However, a similar character state is exhibited by *Gongylidium*

rufipes. While optimization of this character is ambiguous, Farris optimization suggests that the wide paracymbium character state had a common origin in *Gongylidium* and *Sisicottus* (node 10) and was subsequently lost in *Oedothorax*.

Independence.—Since characters come from a small number of character systems and characters within character systems might be linked, non-independence of characters was a concern. However, no two characters had identical distributions across taxa. Since linked characters would be expected to have identical or nearly identical distributions, character non-independence is considered a negligible factor in this analysis.

DISCUSSION

Conflict in erigonine topologies.—The object of appending *Sisicottus* to Hormiga's (in press) analysis was to discover a suitable set of outgroup taxa with which to root the phylogeny of *Sisicottus* species. Despite some instability within the outgroup, relationships among *Sisicottus* species appear to be robustly supported under a wide variety of analytical permutations. My analysis of *Sisicottus* species and their outgroups is not intended to be a test of Hormiga's (in press) phylogenetic hypothesis of erigonine relationships. Although recovery of Hormiga's topology in the outgroup of the *Sisicottus* phylogeny was found to be sensitive to taxon sampling, Hormiga's (in press) topology remains for now the most rigorous hypothesis of erigonine relationships. Nevertheless, it seems clear that systematists should work toward a more robust phylogeny of erigonine relationships by discovering new characters and adding more taxa.

Monophyletic species.—The phylogenetic species concept (Donoghue 1985) has aroused considerable debate (Nelson 1989; de Queiroz & Donoghue 1990; Nixon & Wheeler 1990; Wheeler & Nixon 1990). This concept proposes that the notion of monophyly is applicable to all taxa regardless of rank and that species should therefore be circumscribed on the basis of shared derived similarity. However, cladistic methods are not applicable to resolving tokogenetic relationships. Factors such as polymorphism and unexpressed alleles make this problem intractable. This limitation was discussed by Hennig (1966) and has been leveled as a criticism against the phylogenetic

species concept (Nixon & Wheeler 1990; Wheeler & Nixon 1990). Nevertheless, once a novel character state becomes fixed throughout a population, the resulting autapomorphy constitutes evidence of monophyly in that a character state change occurred in a single common ancestor and subsequently came to exist in all its descendants (Nelson 1989; de Queiroz & Donoghue 1990).

All *Sisicottus* species for which males are known can be diagnosed based on the distal supratregular apophysis alone. The male palpal tibia and the posterior face of the dorsal plate in females are almost as useful taxonomically. Although these characters can be optimized on the tree as autapomorphies, not all *Sisicottus* species have unambiguous character support for monophyly. In a character as rapidly evolving as the distal supratregular apophysis, a unique character state can be assigned to each applicable species. Given the phylogeny of *Sisicottus* in Fig. 115, such a character can be equivocally optimized with between two and all of the states as autapomorphies (no less than one for each sister species pair). Several *Sisicottus* species are supported as monophyletic by unambiguous autapomorphies. These are *S. montigenus* (membranous distal supratregular apophysis, character 3), *S. montanus* (groove in ventral plate, Fig. 64), *S. cynthiae* (large ectal tibial process, Fig. 75; level of ventral margin of dorsal plate, Fig. 77), and *S. aenigmaticus* (posterior face of dorsal plate trapezoidal, character 21; wide ventral plate invagination, Fig. 106; small, widely-spaced spermathecae with narrow margin and narrow copulatory ducts, Fig. 108). Like all *Sisicottus* species for which males are known, *S. quoylei*, *S. panopeus*, *S. crossoclavis*, and *S. orites* have unique distal supratregular apophyses which might represent autapomorphic conditions. However, if each *Sisicottus* species is assigned a unique character state for the form of its distal supratregular apophysis, many character optimizations are possible including the possibility that none of these four species are defined by autapomorphy.

Sisicottus nesides is a special problem, in part because of our ignorance of males of its sister species, *S. aenigmaticus*. Females of *S. nesides* exhibit no autapomorphies. Females of *S. nesides* are almost identical to females *S. orites*. Females of *Sisicottus nesides* and *S. orites* are distinguished only on the basis of

the synapomorphy shared by *S. nesides* and *S. aenigmaticus* (posterior face of dorsal plate with concave sides, character 22). (Although certain quantitative characters are taxonomically useful for separating females of *S. orites* from those of *S. nesides* and *S. aenigmaticus* (Fig. 100), these characters exhibit considerable overlap and cannot be considered as discrete cladistic characters.) *Sisicottus nesides* and *S. aenigmaticus* differ in character states that are unambiguous autapomorphies of *S. aenigmaticus*. Thus, a hypothesis of *S. nesides* as a paraphyletic species cannot be falsified based on females alone. The only character that distinguishes males of *S. nesides* from *S. orites* without overlap is the form of the distal suprategular apophysis. If males of *S. aenigmaticus* are found to have a distal suprategular apophysis like that of *S. orites*, and the discovery of males of *S. aenigmaticus* does not result in a new phylogeny of *Sisicottus*, then *S. nesides* will have an unambiguous autapomorphy supporting its monophyly. If males of *S. aenigmaticus* are found to have a unique distal suprategular apophysis, then *S. nesides* will have ambiguous support for monophyly, just as *S. quoylei*, *S. panopeus*, *S. crossoclavis*, and *S. orites* do. If males of *S. aenigmaticus* are found to share a distal suprategular apophysis form with *S. nesides*, then *S. nesides* will be diagnosed based on plesiomorphic characters and the hypothesis that *S. nesides* is paraphyletic will remain unfalsified.

TAXONOMY

Sisicottus Bishop & Crosby 1938

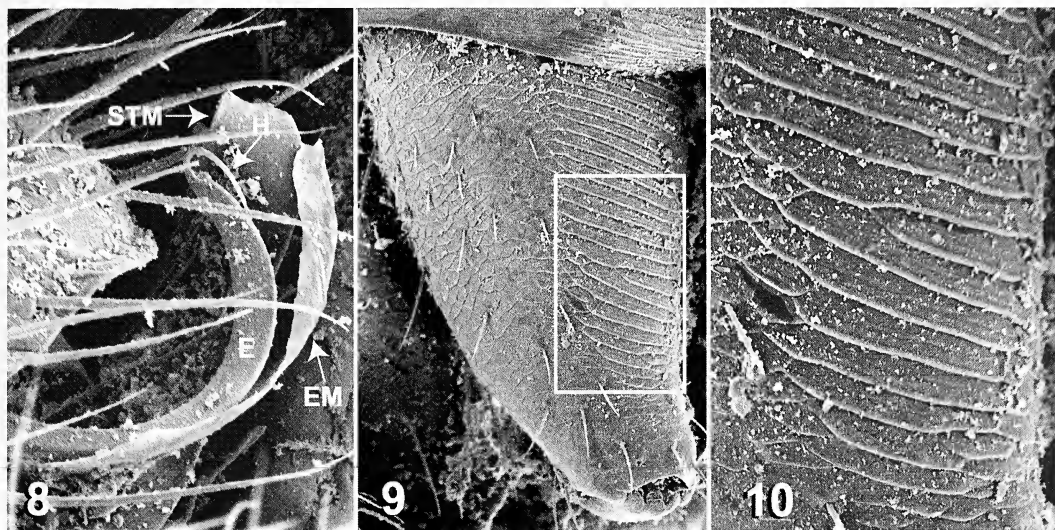
Sisicottus Bishop & Crosby 1938: 57–61. Type species by original designation *Tmeticus montanus* Emerton 1882. Chamberlin & Ivie 1939: 65–66. Roewer 1942: 650. Lowrie & Gertsch 1955: 6. Bonnet 1958: 4065–4066. Holm 1960: 124; 1967: 61. Bragg & Leech 1972: 69. Kaston 1981: 208–209. Brignoli 1983: 356. West et al. 1984: 87. Koponen 1987: 281–283, 285. Crawford 1988: 15. Crawford & Edwards 1988: 437. Jennings et al. 1988: 61, 63. Platnick 1989: 282; 1993: 351; 1997: 427. Aitchison-Benell & Dondale 1990: 224. Dondale et al. 1997: 89.

Etymology.—Bishop & Crosby (1938) did not explain the etymology of *Sisicottus* or any of the other new taxonomic names established therein. It is therefore left to latter-day scholars of nomenclature and classical languages to investigate the meaning of these names. Ac-

cording to H.D. Cameron, the obscure Greek masculine noun *sisys*, known from ancient lexicons and commentaries, is translated as, “any coarse or cheap garment.” This word appears to be the root of three generic names which were erected in Bishop & Crosby 1938. The genus *Sisis* Bishop & Crosby 1938, though not a literal transliteration, is a Latinized derivation of *sisys*. Both *Sisicus* Bishop & Crosby 1938 and *Sisicottus* embellish the same root. Bishop & Crosby do not indicate that the nomenclatural similarity shared by these three genera was meant to imply a hypothesis of phylogenetic affinity. By the rules of zoological nomenclature, *Sisicottus* should be considered an arbitrary combination of letters with has the form of a masculine Latin word (Art. 11b.iii, International Commission on Zoological Nomenclature 1985).

Diagnosis.—*Sisicottus* males differ from other erigonine genera with a long, single turn spiral embolus by the presence of a paracymbium in the form of a wide plate in ventral view (Fig. 60, character 14), a hook recurved over the aperture at the tip of the embolus (Fig. 8, character 2), an anteriorly projecting suprategular membrane (Fig. 42, character 6), a straight, tapered marginal suprategular apophysis (Figs. 95, character 6), a conspicuous distal suprategular apophysis that lies across part of the tegulum in ectal view (Figs. 61, 93, character 4), a glabrous excavation on the mesal side of the cymbium near the palpal tibia (Fig. 59, character 15), a lamella characteristic in the shape of a comma (Fig. 59, character 9), the absence of a radical tailpiece (character 7), a palpal tibial apophysis originating from the mesal side (Fig. 62), and by the presence of a protegulum with scale like papillae and a tegular sac arising from the tegulum (Figs. 46, 60, characters 12, 13). Females can be distinguished from other erigonine genera with complete encapsulation of the copulatory ducts (character 28) by the small copulatory duct openings (Fig. 65, character 25), the origin of the copulatory ducts from the ectal side of the spermathecae (Fig. 65, character 26), and the path of the copulatory ducts which initially project anteriorly from the spermathecae then turn to pass between the spermathecae and terminate at copulatory openings near the epigastric furrow (Fig. 65, character 27).

Description.—Small to medium-sized eri-



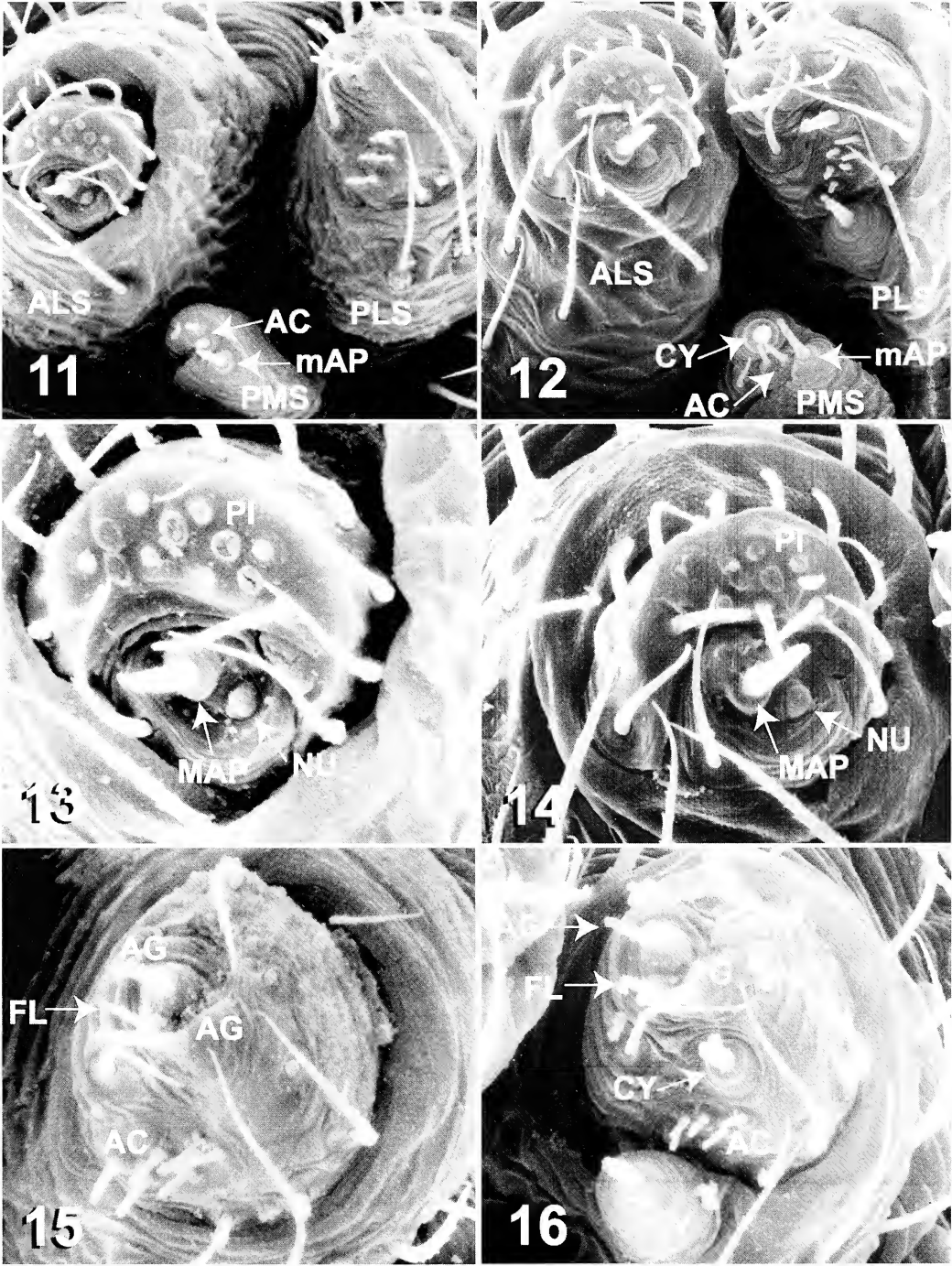
Figures 8–10.—Scanning electron micrographs of *Sisicottus panopeus* from Lake Louise, Alberta. 8, Ectal view of right palpus showing embolic hook; 9, 10, Left chelicera of male.

gonine spiders (carapace length = 0.67–1.24 mm). Carapace usually orange with dusky highlights, darker in ocular region; glabrous except for several rigid setae in line between thoracic groove (itself little more than a narrow line of darker pigment) and ocular area (which is clothed in fine setae) (Fig. 6). Sternum and labium darker than carapace; legs and palpi often slightly lighter. Chelicerae of both sexes with imbricated stridulatory files (Figs. 9, 10; Hormiga in press); small plectra visible near base of palpal femora. Fang furrow armed with usually five large anterior teeth and 4–5 minute posterior teeth. Palpal tibiae of both sexes with one prolateral and two retrolateral trichobothria. Tibiae of legs I–III with two dorsal macrosetae; fourth tibia with only proximal macroseta. Metatarsal trichobothria present on legs I–III; absent from leg IV. Tml usually ranges between 0.44–0.65 (range of mean plus or minus one standard deviation values; Fig. 7; Tables 2, 3); variation appears constant across sexes, species, and individuals. Main tarsal claws with several teeth; auxiliary claw with single preterminal tooth (Fig. 109).

Abdomen usually uniform dark to light grey and clothed in fine setae. Anterior lateral spinnerets with 9–13 piriform spigots, a single major ampullate spigot, and a nubbin in both sexes (Figs. 13, 14); posterior lateral spinnerets with 4–7 aciniform spigots, two aggregate

spigots, and one flagelliform spigot plus two cylindrical spigots in females only (Figs. 15, 16); posterior median spinnerets with one minor ampullate spigot, two aciniform spigots, and, in females, one cylindrical spigot (Figs. 11, 12). Tracheae desmitracheate (Millidge 1984a); median trunks with many tracheoles that pass through the pedicel; lateral trunks unbranched and confined to abdomen; tracheoles of uniform diameter and without taenidia (*sensu* Blest 1976); spiracle a single slit-like opening, somewhat rounded laterally (Fig. 4).

Males: Embolus sclerotized and rigid, describing single spiral turn; arises from radix on mesal side of bulb, passes under alveolus, and associates distally with an embolic membrane and a suprategular membrane (Fig. 42), and terminates in a hook (Figs. 3, 8). Radix closely joined to lamella characteristica by membrane (Figs. 1, 3). Radical tailpiece absent. Distal suprategular apophysis ribbon-like, membranous to heavily sclerotized, lying across tegulum in ectal view (Fig. 61). Straight, tapered marginal suprategular apophysis varies little in shape, orientation, or relative length (Fig. 42). Paracymbium with three macrosetae (occasionally four) arising near cymbial margin (Fig. 61); formed into wide plate in ventral view with single macroseta (occasionally two) arising centrally (Fig. 60). Protégulum semitransparent to opaque with ectal apex; tegular sac arises from mesal



Figures 11–16.—Scanning electron micrographs showing spinneret spigot morphology, left side. 11, 13, 15, Male *Sisicottus nesides* from Primrose Camp, Alaska. 12, 14, Female *S. montanus* from Mt. Mainsfield, Vermont. 16, Female *S. crossoclavis* from Deemer Creek, Washington; 11, 12, Spinnerets; 13, 14, Anterior lateral spinnerets; 15, 16, Posterior lateral spinnerets.

side (Fig. 46); scale-like papillae cover much of protegulum. Glabrous area near base of cymbium on mesal side set apart by fine sclerotized ridge (Fig. 59). Palpal tibia with mesal apophysis that is often curved ectally (Fig. 62), although it is very short and not distinctly curved in some species (Fig. 20). Clusters of macrosetae occur on ectoventral quarter of palpal tibia (Fig. 5) and distal part of cymbium.

Females: Epigynum a ventral plate and dorsal plate. In ventral view, ventral plate often with median invagination at posterior margin revealing dorsal plate below (Figs. 28, 87). Dorsal plate folded posteriorly at right angle to ventral plate where it forms a surface (the DPP) that can be of diagnostic value at the species level. Single pair of spermathecae situated near posterior margin of epigynum (Fig. 65). Copulatory ducts usually thick proximally, narrow distally, and encapsulated; they arise from ectal half of spermathecae, travel mesally across spermathecae, run anteriorly, then double back to terminate as copulatory openings near posterior margin of epigynum between spermathecae (Fig. 65). Fertilization ducts lightly sclerotized, sinuous or looped, and arising from the mesal region of spermathecae (Figs. 65, 98). Fertilization ducts terminate at dorsal margin of epigynum near anterior extension of dorsal fold of dorsal plate.

Natural history.—Most of what is known about the natural history of these spiders comes from brief remarks in papers on spider ecology and distribution (Koponen 1987; Crawford 1988; Crawford & Edwards 1988; Jennings et al. 1988; Aitchison-Benell & Dondale 1990) and in the form of notes written by collectors on data labels. Data labels indicate that these spiders are usually associated with wet moss, leaf litter, or other ground microhabitats in boreal forests and bogs. Occa-

sionally, they are beaten off arboreal, woody, or herbaceous vegetation or swept from meadow vegetation. The data label for a series of *S. crossoclavis* new species from Washington reports finding one adult female in a web. The capture of two male *S. nesides* from British Columbia in a flight intercept trap suggests that adult male *Sisicottus* may disperse by ballooning. The extraction of a female *S. cynthiae* new species from the stomach of a newt offers a hint as to one role these spiders play in the trophic structure of their communities.

Distribution.—In North America: Canada, Alaska, eastern United States south to North Carolina and Tennessee, and western United States south to California, Arizona, and New Mexico. In Asia, currently known only from the Kuril Islands.

Composition.—Nine species: *Sisicottus montigenus* Bishop & Crosby 1938, *S. quoylei* new species, *S. montanus* (Emerton 1882), *S. panopeus* new species, *S. crossoclavis* new species, *S. cynthiae* new species, *S. orites* (Chamberlin 1919), *S. nesides* (Chamberlin 1921) and *S. aenigmaticus* new species.

Misplaced species.—Examination of the type specimens of *Sisicottus uintanus*, *S. cornuella*, *S. atypicus* Chamberlin & Ivie (1944) (all in AMNH), and *S. hibernus* (OSU) confirms that none of these species belong to *Sisicottus*. *Sisicottus uintanus* is formally transferred to *Typhochrestus* (NEW COMBINATION). See also taxonomic history section above.

Sisicottus uintanus Chamberlin & Ivie 1939: 65, figs. 31–34 [♂, ♀] = *Typhochrestus uintanus*.
NEW COMBINATION.

Sisicottus cornuella Chamberlin & Ivie 1939: 65–66, figs. 35–37 [♂] = *Walckenaeria cornuella*.
Transfer by Millidge 1983.

Sisicottus atypicus Chamberlin & Ivie 1944: 76–77, figs. 139, 140 [♂] = *Souessoula parva* (Banks).
Synonymy by Ivie 1967.

Sisicottus hibernus Barrows 1945:74, figs. 1, 2 [♂] = *Carorita hiberna*. Transfer by Zujko-Miller (1999).

KEY TO SPECIES OF THE GENUS *SISICOTTUS*

Males

(note: male of *S. aenigmaticus* is unknown)

- 1. Distal suprategular apophysis heavily sclerotized (Fig. 93, DSA). Western North America 2
- Distal suprategular apophysis membranous to lightly sclerotized (Fig. 61, DSA). Asia, eastern or western North America 5
- 2 (1).Terminus of distal suprategular apophysis widened with serrated margin (Fig. 67, DSA). Ectal tibial process absent (Fig. 68) *crossoclavis* new species

- Terminus of distal supratregular apophysis flat to wavy or bifid with two pointed apices; not more than slightly widened distally. Ectal tibial process prominent (Fig. 94) 3
- 3 (2). Terminus of distal supratregular apophysis bifid with two pointed apices, the inner more pronounced than the outer (Figs. 84, 102, DSA) *nesides* (Chamberlin 1921)
- Terminus of distal supratregular apophysis flat to wavy; never with pointed apices 4
- 4 (3). Terminus of distal supratregular apophysis with wavy margin (Figs. 73, 80, DSA). Palpal tibia with large ectal tibial process and short palpal tibial apophysis (palpal tibial apophysis length < 0.09 mm; Fig. 75, ETP, PTA) *cynthiae* new species
- Terminus of distal supratregular apophysis flat or with two rounded lobes (Fig. 92, DSA). Palpal tibia with short ectal tibial process and long palpal tibial apophysis (palpal tibial apophysis length > 0.12 mm; Fig. 94, ETP, PTA) *orites* (Chamberlin 1919)
- 5 (1). Distal supratregular apophysis extends to ventral midline of palpal bulb (Fig. 19). Palpal tibial apophysis very short (palpal tibial apophysis length < 0.04 mm; Fig. 20, PTA). Eastern North America 6
- Distal supratregular apophysis extends about half way down palpal bulb (Fig. 61). Palpal tibial apophysis longer (palpal tibial apophysis length > 0.04 mm; Fig. 62, PTA). Asia, eastern or western North America 7
- 6 (5). Distal supratregular apophysis membranous; inner margin strongly convex; terminal margin serrated (Figs. 19, 26). North Carolina and Tennessee *montigenus* Bishop & Crosby 1938
- Distal supratregular apophysis moderately sclerotized; inner margin sinuous; terminus a sharp apex (Fig. 34). Northeastern United States, southeastern Canada *quoylei* new species
- 7 (5). Palpal tibial apophysis short (palpal tibial apophysis length < 0.08 mm); ectal tibial process present (Fig. 62, ETP). Distal supratregular apophysis extends ventrally beyond level of supratregular membrane (Figs. 47, 61, DSA). Less than 6 macrosetae in cluster on ectal side of palpal tibia. Widespread in North America *montanus* (Emerton 1882)
- Palpal tibial apophysis long (palpal tibial apophysis length > 0.08 mm); ectal tibial process absent (Fig. 41). Distal supratregular apophysis does not extend ventrally beyond level of supratregular membrane (Figs. 40, 45, DSA). More than 7 macrosetae in cluster on ectal side of palpal tibia. Western North America and Asia *panopeus* new species

Females

1. Ventral plate of epigynum with deep invagination (ventral plate invagination depth < 0.04 mm; Fig. 96, VP) 2
- Ventral plate of epigynum with invagination shallow or absent (ventral plate invagination depth < 0.04 mm; Figs. 63, 76, VP) 6
- 2 (1). Posterior face of dorsal plate narrow (width of posterior face of dorsal plate < 0.12 mm), subrectangular with convex lateral margins (Fig. 37, DPP). Dorsal fold of dorsal plate membranous. Lateral margin of epigynal capsule straight (Fig. 38, CDC). Carapace small (carapace length < 0.80 mm). Eastern North America 3
- Posterior face of dorsal plate wide (width of posterior face of dorsal plate > 0.12 mm), triangular or trapezoidal with straight to concave lateral margins (Fig. 97, DPP). Dorsal fold of dorsal plate sclerotized, trapezoidal, widest posteriorly. Lateral margin of epigynal capsule strongly bowed (Fig. 98, CDC). Carapace large (carapace length > 0.86 mm). Western North America 4
- 3 (2). Ventral plate invagination wide and very deep (ventral plate invagination width > 0.06 mm; ventral plate invagination depth > 0.09 mm; Fig. 22, VPIW, VPID) *montigenus* Bishop & Crosby 1938
- Ventral plate invagination narrow and only moderately deep (ventral plate invagination width < 0.05 mm, ventral plate invagination depth < 0.09 mm; Fig. 36) *quoylei* new species
- 4 (2). Ventral plate invagination wide (ventral plate invagination width ca. 0.06 mm). Posterior face of dorsal plate trapezoidal (Fig. 107, DPP) *aenigmaticus* new species
- Ventral plate invagination narrow (ventral plate invagination width < 0.05 mm). Posterior face of dorsal plate triangular (Figs. 97, 105, DPP) 5
- 5 (4). Posterior face of dorsal plate with lateral margins never more than slightly concave (Fig. 97,

- DPP). Epigynum long (epigynum length = 0.152–0.209 mm). Copulatory duct capsule wide (copulatory duct capsule width = 0.143–0.238 mm) *orites* (Chamberlin 1919)
- Posterior face of dorsal plate with concave lateral margins (Fig. 105, DPP). Epigynum short (epigynum length = 0.133–0.181 mm). Copulatory duct capsule narrow (copulatory duct capsule width = 0.100–0.176 mm) *nesides* (Chamberlin 1921)
- 6 (1). Dorsal fold of dorsal plate membranous (Fig. 65, DF) 7
- Dorsal fold of dorsal plate sclerotized, trapezoidal, widest posteriorly (Fig. 71, DF) 8
- 7 (6). Ventral plate enfolded forming broad groove (Figs. 53, 54, G). Posterior face of dorsal plate triangular with sharply pointed ventral margin (Fig. 64, DPP). Eastern or western North America *montanus* (Emerton 1882)
- Ventral plate without groove (Figs. 51, 52). Posterior face of dorsal plate subrectangular with flat ventral margin (Fig. 44, DPP). Western North America and Asia *panopeus* new species
- 8 (6). Ventral margin of posterior face of dorsal plate dorsal to ventral extent of spermathecae (Fig. 77, DPP). Posterior margin of copulatory duct capsule oriented anteriorly (Fig. 78, CDC). Oregon *cynthiae* new species
- Ventral margin of posterior face of dorsal plate about level with ventral extent of spermathecae (Fig. 70, DPP). Posterior margin of copulatory duct capsule oriented posteriorly (Fig. 71, CDC). Western North America *crossoclavis* new species

Sisicottus montigenus Bishop & Crosby
1938
Figs. 17–28, 31, 32

Sisicottus montigenus, in part: Bishop & Crosby 1938: 60–61, figs. 10–11 [♂, ♀]. Roewer 1942: 650. Bonnet 1958: 4066. 3♂4♀ syntypes from UNITED STATES: North Carolina, Yancey County, Mt. Mitchell, 12 October 1923, in AMNH, examined.

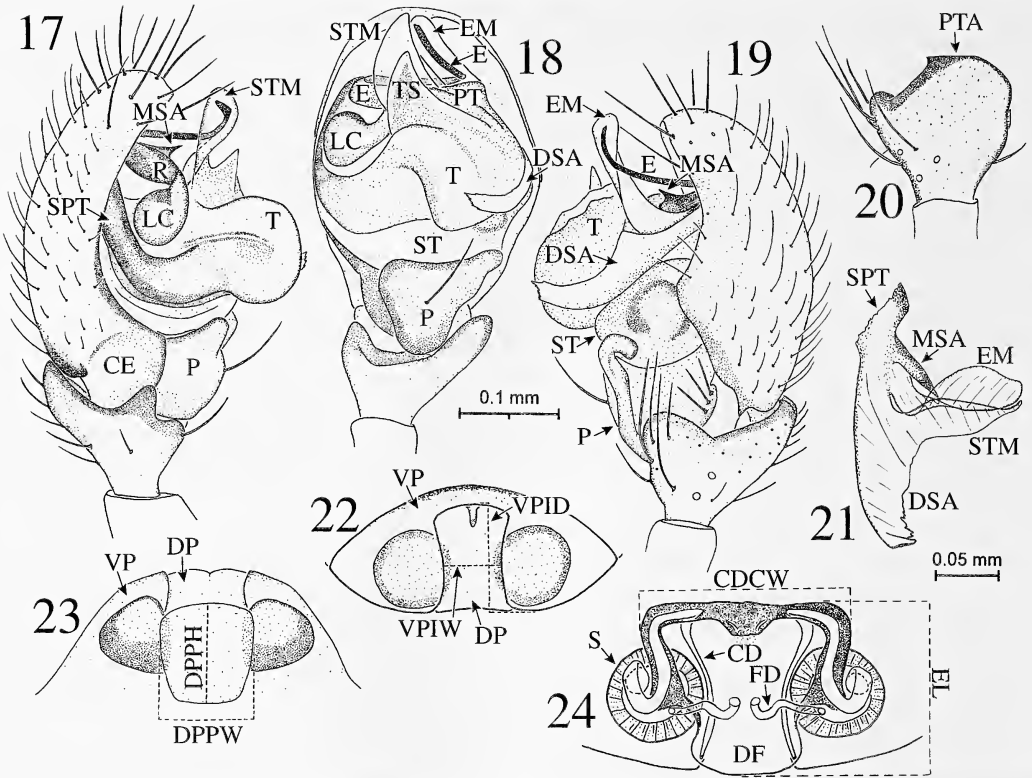
Diagnosis.—Males of *S. montigenus* are distinguished from those of all other *Sisicottus* species except its sister species, *S. quoylei*, by the form of the palpal tibial apophysis, which is quite short with a flat distal margin and no ectal tibial process (Fig. 20, characters 16, 17). The form of the distal supratרגular apophysis is unique among *Sisicottus*, being membranous and quite transparent, extending to near the ventral midline of the palpal bulb with variable amounts of serration along the margin, especially in the near terminus (Figs. 25–27, characters 3, 4). This characteristic is the most reliable way to distinguish this species from all other *Sisicottus* species including *S. quoylei*.

Females of *S. montigenus* have a ventral plate invagination that is almost always deeper than any other *Sisicottus* species (Fig. 22). They can be distinguished from other species with a deep ventral plate invagination, except *S. quoylei*, by the posterior face of the dorsal plate, which is subrectangular (Fig. 23, character 21) and the membranous dorsal fold of the dorsal plate (Fig. 24, character 24). The

ventral plate invagination is wider than any species except *S. aenigmaticus* (Table 3). *Sisicottus montigenus* can be distinguished from all species except *S. quoylei* by the form of the anterior margin of the capsule which is nearly flat rather than formed into two convex lateral lobes (Fig. 24, character 30). Depth and width of the ventral plate invagination reliably separate *S. montigenus* from its sister species, *S. quoylei* (Fig. 31).

Description.—Small (carapace length = 0.67–0.80 mm); coloration much darker than in other *Sisicottus* species. Distal supratרגular apophysis of male palpus membranous, long, extends to near ventral midline of palpal bulb; with serrated outside and terminal margins (Figs. 25–27). Palpal tibia short; palpal tibial apophysis short with flat distal margin and no ectal tibial process (Fig. 20); sparse cluster of macrosetae (3–7) on ectal side of palpal tibia. Females with deep and wide invagination of ventral plate of epigynum (Figs. 22, 31). Posterior face of dorsal plate generally rectangular, usually slightly taller than wide with a flat or slightly convex ventral margin (Fig. 23). Dorsal fold of dorsal plate membranous. Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule nearly flat; fertilization ducts sinuous (Fig. 24). See Tables 2–4.

Natural history.—*Sisicottus montigenus* has been collected exclusively in high elevation spruce and Fraser fir forests of the southern Appalachian mountains. Over the last decade, much of this habitat has been severely



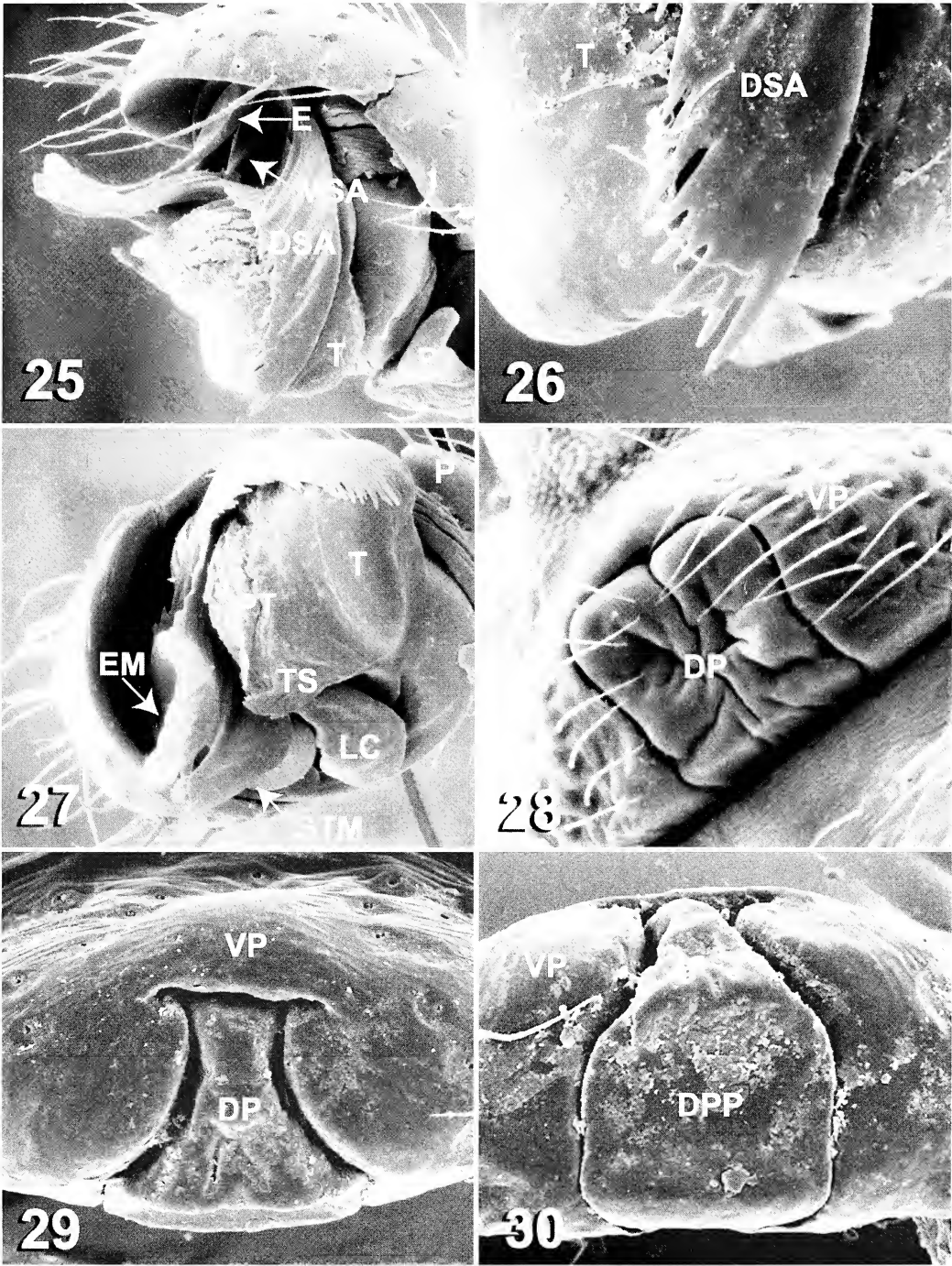
Figures 17–24.—*Sisicottus montigenus* with limits of some quantitative characters. 17–20, Palpus of male from Mt. Mitchell, North Carolina. 17, Mesal view; 18, Ventral view; 19, Ectal view; 20, Palpal tibia, dorsal view; 21, Suprategulum separated from palpus of male from Clingman's Dome, North Carolina, ectal view; 22, 23, Epigynum of female from Mt. Mitchell, North Carolina. 22, Ventral view; 23, Posterior view. 24, Cleared epigynum from Clingman's Dome, North Carolina, dorsal view. Scales: Figs. 21, 24 = 0.05 mm; other figures = 0.1 mm.

altered. The extensive damage to these forests has been blamed principally on the balsam wooly adelgid, *Adelges piceae* Ratzeburg (Homoptera: Adelgidae), an introduced European pest of firs. *Sisicottus montigenus* is usually associated with ground microhabitats, particularly mosses, but has also been taken on beating sheets. In one collection from Clingman's Dome, North Carolina in 1977, *S. montigenus* was the most abundant spider species. However, my repeated collecting efforts at this now much altered locality (Wheeler & McHugh 1994; F. Coyle pers. comm.) have failed to produce additional specimens. This apparent rapid change in population size in response to environmental degradation suggests that this species may be worthy of consideration for federal protection as a threatened or endangered species.

Distribution.—North Carolina and Tennessee; restricted to high elevation spruce-fir for-

ests (Fig. 32). A record from Michigan is almost certainly erroneous (Drew 1967), although this site is not very far outside the currently recognized range of *S. quoylei*. Any *Sisicottus* that Drew may have collected appear to be lost; no *Sisicottus* specimens can be found in the Michigan State University Entomology Museum (R.J. Snider pers. comm.).

Material examined.—UNITED STATES: *North Carolina*: Mitchell County., Roan High Bluff, 6200 feet, in moss from rocks in spruce-fir forest, 17 November 1978, 1♂5♀ (F. Coyle & D. Pittillo, FAC); Swain County, Clingman's Dome, 6600 feet, in moss from spruce-fir forest floor, 6 November 1977, 9♂26♀ (F. Coyle, FAC); Mt. Mitchell, 6600 feet, in moss from spruce-fir forest floor, 20 October 1977, 3♂12♀ (F. Coyle, FAC); Mt. Mitchell, 6600 feet, in moss from rock ledges in spruce-fir forest, 20 October 1977, 7♀ (F. Coyle, FAC). *Tennessee*: Sevier County, GSMNP, Mt. LeConte, 100 m below spring along Trillium Gap



Figures 25–30.—Scanning electron micrographs of *Sisicottus montigenus* and *S. quoylei*. 25–28, *S. montigenus* from Mt. Mitchell, North Carolina. 25, Palpus, ectal view; 26, Terminus of distal suprategular apophysis; 27, Palpus, ventral view; 28, Epigynum, ventral view. 29, 30, Epigynum of female *S. quoylei* from Mt. MacIntyre, New York. 29, Ventral; 30, Posterior.

Tr., UTM: N394833 E27913, 6300 feet, beating 14:20–15:20 in 25 yr-old fir forest, 19 July 1995, 1♂3♀ (Coyle, Williams & Carbiener, GSMNP); Mt. LeConte, 35°37'N, 83°27'W, 5♂10♀ (AMNH).

Sisicottus quoylei new species

Figs. 29–38

Sisicottus montigenus, in part: Bishop & Crosby 1938: 60–61, fig. 9 [♂]. Roewer 1942: 650. Bonnet 1958: 4066.

Types.—Male holotype with one female paratype from CANADA: Newfoundland, King's Point, beating black spruce, 19 August 1984, L. Hollett, deposited in CNC.

Etymology.—Named for the protagonist in E. Annie Proulx's Pulitzer Prize winning novel, *The Shipping News*, which is set within the range of this species. The name is also a homonym of the patronymic that would result from a species named for Dr. Frederick A. Coyle, my master's thesis advisor.

Diagnosis.—Males of *S. quoylei* are distinguished from those of all other *Sisicottus* species except its sister species, *S. montigenus*, by the form of the palpal tibial apophysis, which is quite short with a flat distal margin and no ectal tibial process (Fig. 35, characters 16, 17). It is separated from *S. montigenus* males by a moderately sclerotized distal supratetral apophysis (membranous in *S. montigenus*) which tapers to a single sharp terminal apex on its inside margin (Fig. 34, character 3).

Females of *S. quoylei* are distinguished from all other *Sisicottus* species except *S. montigenus* by the form of the anterior margin of the capsule which is nearly flat rather than formed into two convex lateral lobes (Fig. 38, character 30). They are separated from *S. montigenus* by the form of the ventral plate invagination which is wider and deeper in *S. montigenus* (Figs. 31, 38). Females of *S. quoylei* have a ventral plate invagination that is deeper than that of *S. montanus*, *S. panopeus*, *S. crossoclavis*, or *S. cynthiae* (character 19). They can be distinguished from other species with a deep ventral plate invagination, except *S. montigenus*, by having a dorsal plate with a subrectangular rather than triangular or trapezoidal posterior face (Fig. 37, character 21), and by the dorsal fold of the dorsal plate, which is membranous rather than sclerotized (Fig. 38, character 24).

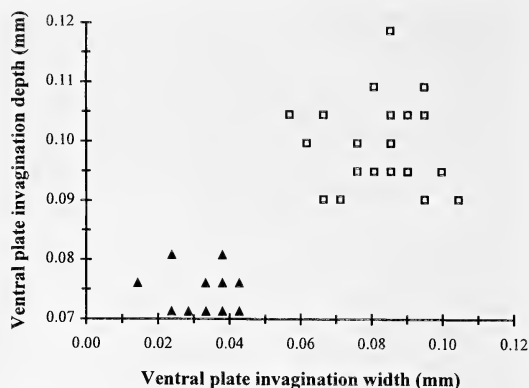


Figure 31.—Scattergram of ventral plate invagination depth plotted against ventral plate invagination width for females of *Sisicottus montigenus* (●) and *S. quoylei* (▲).

Description.—Small (carapace length 0.71–0.82 mm); coloration typical (see description section for *Sisicottus*). Distal supratetral apophysis of male palpus moderately sclerotized, long, extends to near ventral midline of palpal bulb; terminus pointed (Fig. 34). Palpal tibia short; palpal tibial apophysis short with flat distal margin without ectal tibial process (Fig. 35); sparse cluster of macrosetae (3–6) on ectal side of palpal tibia. Females with deep and narrow invagination of ventral plate of epigynum (Fig. 36). Posterior face of dorsal plate generally rectangular, usually slightly taller than wide with convex ventral margin (Fig. 37). Dorsal fold of dorsal plate membranous. Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule nearly flat; fertilization ducts sinuous (Fig. 38). See Tables 2–4.

Natural history.—Locality labels indicate that this species is associated with conifer forests, especially balsam fir. It is sympatric with *S. montanus* over at least part of its range.

Distribution.—New Brunswick, Newfoundland, Nova Scotia, and New York (Fig. 32).

Material examined.—CANADA: *New Brunswick*: Green River, 30 mi N. Edmundston, balsam fir, 6 June 1959, 1♂1♀ (T.R. Renoult, CNC), balsam fir, 30 June 1965, 1♂ (T.R. Renoult, CNC); Kedgwick River, balsam fir, 27 June 1966, 1♀ (T.R. Renoult, CNC). *Newfoundland*: Bottom Brook, beating balsam fir, 15 August 1984, 1♂ (L. Hollett, CNC); Gallants, fir foliage, 23 June 1982, 1♂ (K.P. Lim, CNC); Hampden, beating balsam fir, 14 June

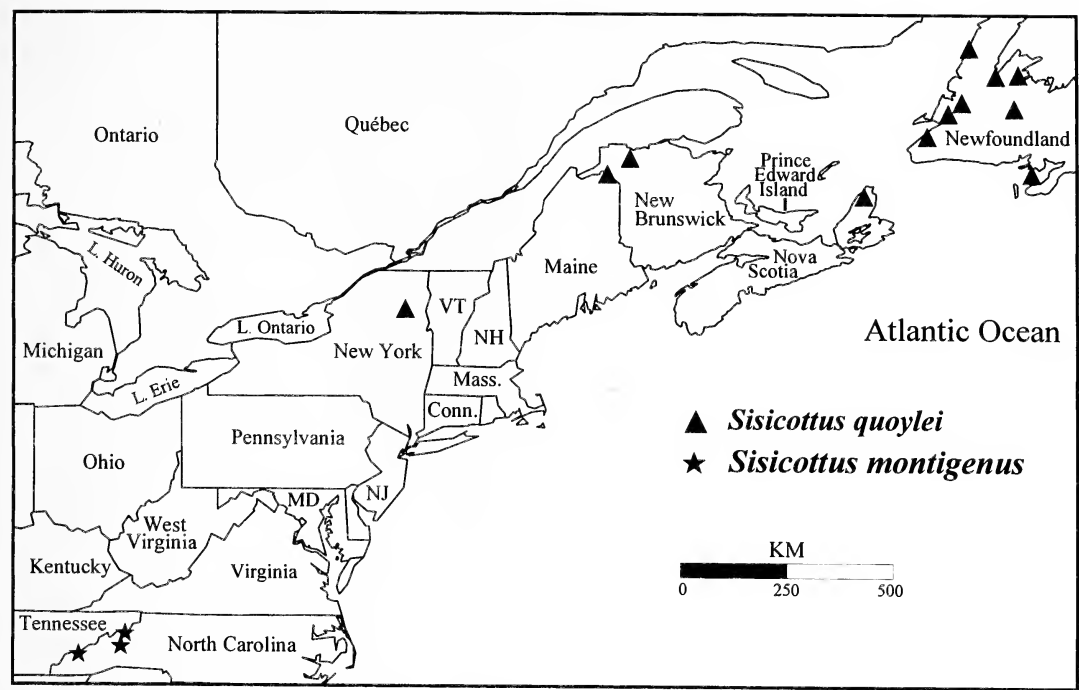
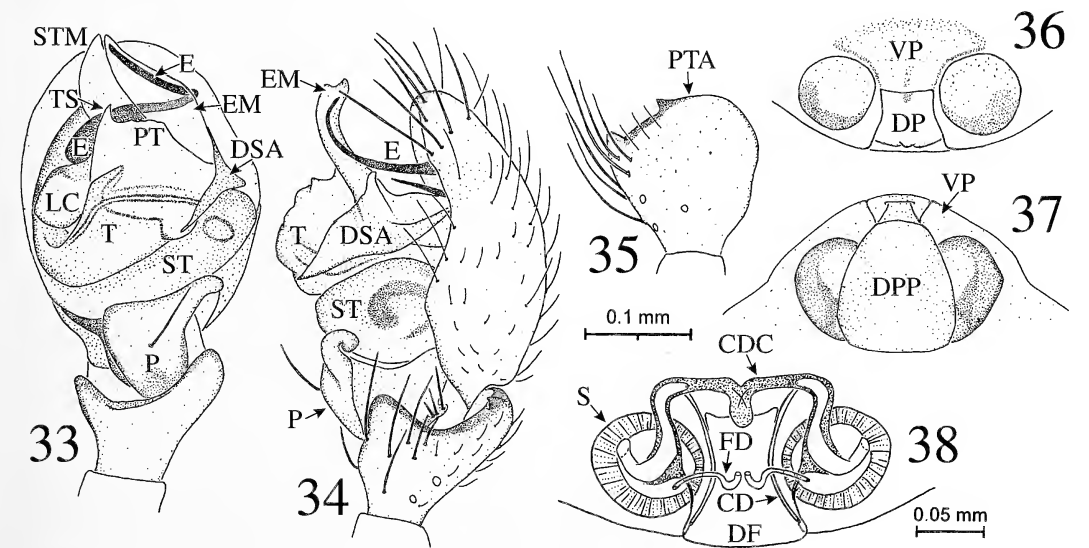


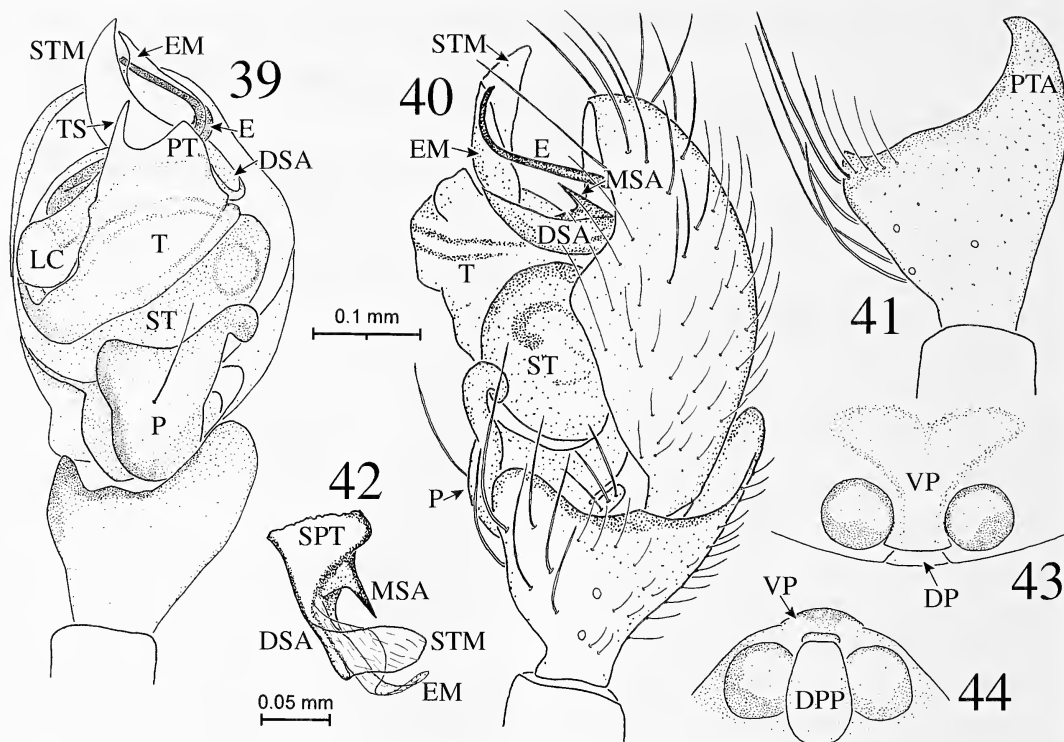
Figure 32.—Eastern United States and southeastern Canada, showing distribution of *Sisicottus montigenus* (★) and *S. quoylei* (▲).

1977, 1 ♀ (CNC); Noel Pauls Brook, *ex Abies balsamea*, 26 June 1977, 1 ♀ (L. Hollett, CNC), *ex Abies balsamea*, 8 August 1977, 1 ♂ (L. Hollett, CNC), *Abies balsamea*, July 1984, 1 ♀ (L. Hollett, CNC); Paddys Brook, 10 mi. W St. Johns, November

1982–April 1983, 1 ♀ (D.W. Langer, CNC); Portland Creek, June 1974, 1 ♀ (Heinrich, CNC); Steady Brook, 48°57'N, 57°50'W, beating balsam fir, 17 August 1984, 1 ♀ (L. Hollett, CNC); St. Fintans, 30 June 1942, 1 ♀ (E.J. Gillan, CNC). Nova Scotia:



Figures 33–38.—*Sisicottus quoylei* from King's Point, Newfoundland. 33, Palpus, ventral view; 34, Palpus, ectal view; 35, Palpal tibia, dorsal view; 36, Epigynum, ventral view; 37, Epigynum, posterior view; 38, Cleared epigynum, dorsal view. Scales: Fig. 38 = 0.05 mm; all others = 0.1 mm.



Figures 39–44.—*Sisicottus panopeus* from Mt. Rainier, Washington. 39–42, Male palpus. 39, Ventral view; 40, Ectal view; 41, Palpal tibia, dorsal view; 42, Suprategulum separated from palpus, ectal view. 43, 44, Epigynum. 43, Ventral view; 44, Posterior view. Scales: Fig. 42 = 0.05 mm; all others = 0.1 mm.

Cape Breton Highlands National Park, North Mountain, 46°48'N, 60°41'W, ex fen-pans, 8 June 1983, 1♀ (H. Goulet, CNC). **UNITED STATES:** New York: Lake Tear, Mt. Marcy, 4 September 1922, 1♂ (Bishop, AMNH); Mt. MacIntyre, 1 July 1923, 1♂1♀ (Crosby, AMNH).

***Sisicottus panopeus* new species**

Figs. 39–46, 51, 52, 57, 58

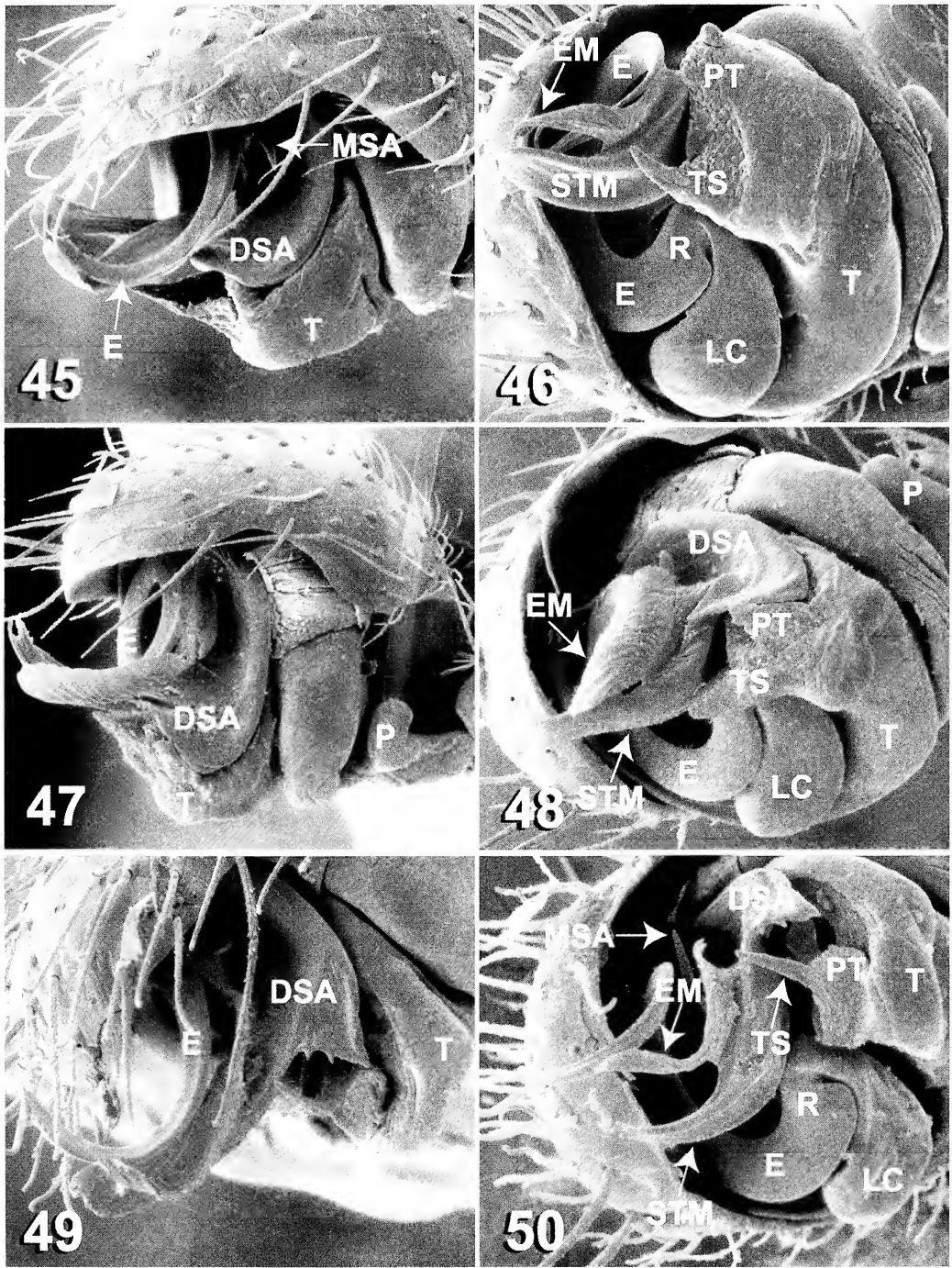
Sisicottus montanus: Lowrie & Gertsch 1955: 6 (misidentification). Holm 1960: 124 (misidentification). Bragg & Leech 1972: 69 (misidentification). Crawford 1988: 15 (in part). Crawford & Edwards 1988: 437, figs. 21–22 [♀] (misidentification). Platnick 1993: 351.

Types.—Male holotype from UNITED STATES: Washington, Mt. Rainier National Park, Paradise, 46°48'N, 121°44'W, 12 September 1965, J. & W. Ivie, deposited in AMNH.

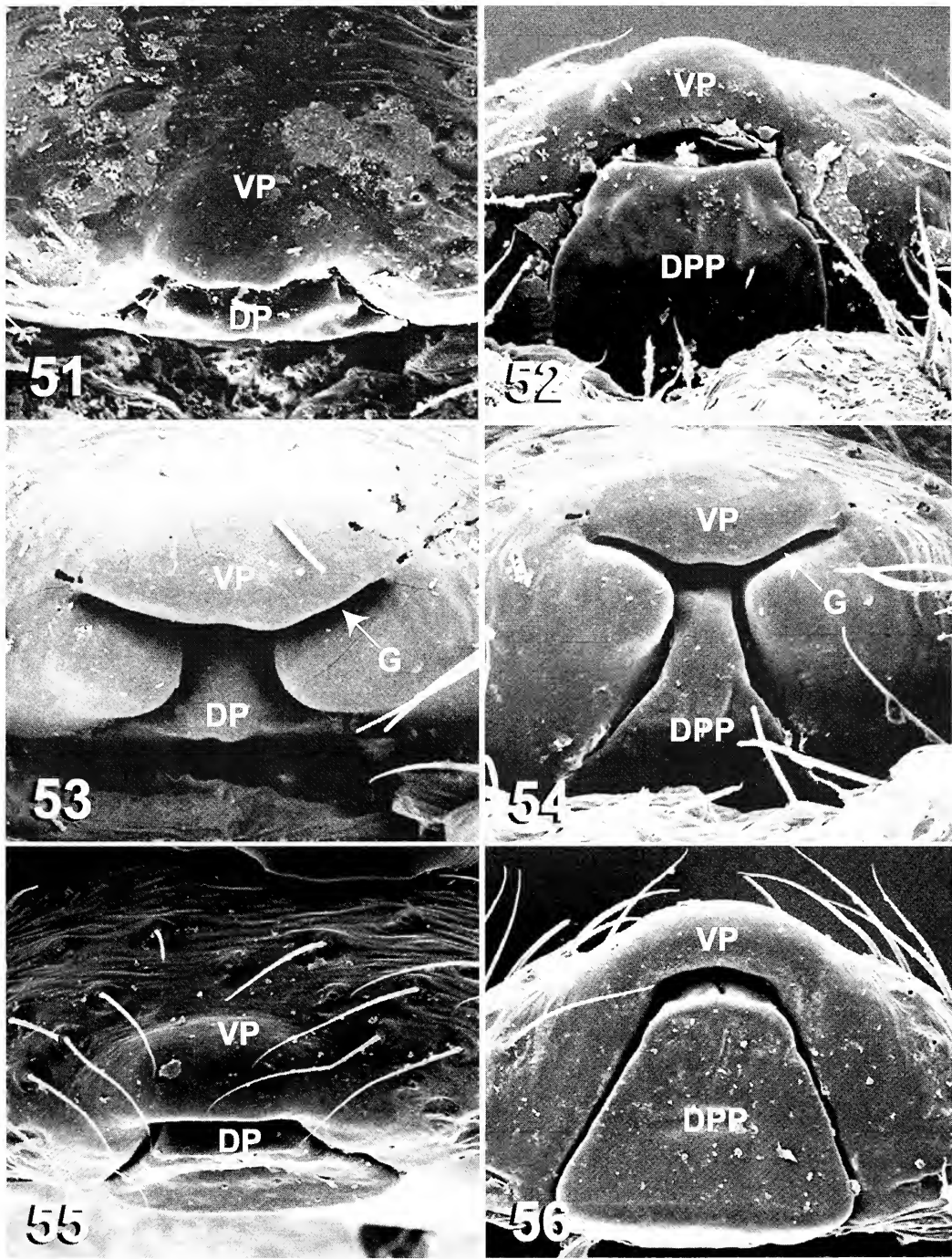
Etymology.—Derived from the monotypic mollusc genus *Panope*; *P. generosa*, the geoduck clam, is the mascot of my alma mater, The Evergreen State College.

Diagnosis.—Males of *S. panopeus* share

with *S. montanus* and *S. crossoclavis* a distal suprategular apophysis that extends about half way down the ectal side of the palpal bulb (Fig. 40, character 4); in all other *Sisicottus* species, the distal suprategular apophysis extends to near the ventral midline of the palpal bulb. They are distinguished from *S. montanus* by their longer palpal tibia and palpal tibial apophysis (Figs. 41, 57), by the lack of an ectal tibial process (Fig. 41, character 17), by the presence of more macrosetae in their ectal tibial cluster (7–11 in *S. panopeus*, 2–6 in *S. montanus*), and by the form of the distal suprategular apophysis which projects ventrally past the level of the suprategular membrane in *S. montanus* (Figs. 47, 61) but stops near the level of the suprategular membrane in *S. panopeus* (Figs. 40, 45). *Sisicottus crossoclavis* can be distinguished from both of these species by its heavily sclerotized distal suprategular apophysis with a serrated terminal margin (Fig. 67, character 3); *S. panopeus* and *S. montanus* have a moderately sclerotized distal suprategular apophysis with a rounded terminal margin (Fig. 40).



Figures 45–50.—Scanning electron micrographs of *Sisicottus* palpi. 45, 46, *S. panopeus* from Mt. Rainier, Washington. 45, Ectal view; 46, Ventral view. 47, 48, *S. montanus* from Mt. Mansfield, Vermont. 47, Ectal view; 48, Ventral view. 49, 50, *S. crossoclavis* from Rabbit Creek, Washington. 49, Ectal view detailing distal supratarsal apophysis; 50, Ventral view.



Figures 51–56.—Scanning electron micrographs of *Sisinottus* epigyna. 51, 52, *S. panopeus* from Lake Louise, Alberta. 51, Ventral view; 52, Posterior view. 53, 54, *S. montanus* from Piscataquis County, Maine. 53, Ventral view; 54, Posterior view. 55, 56, *S. crossoclavus* from Deemer Creek, Washington. 55, Ventral view; 56, Posterior view.

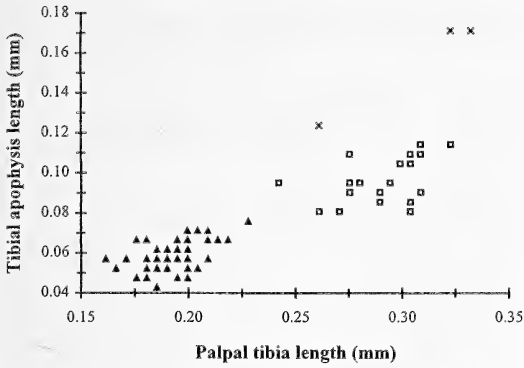


Figure 57.—Scattergram of palpal tibial apophysis length plotted against palpal tibia length for males of *Sisicottus panopeus* (●), *S. montanus* (▲), and *S. crossoclavis* (×).

Females of *S. panopeus*, like those of *S. montanus*, *S. crossoclavis*, and *S. cynthiae*, have a shallow ventral plate invagination (Fig. 43, character 19); this separates them from females of *S. montigenus*, *S. quoylei*, *S. orites*, *S. nesides*, and *S. aenigmaticus*. *Sisicottus panopeus* is unique among species with a shallow ventral plate invagination in having a dorsal plate with a posterior face that is subrectangular with a flat ventral margin (Fig. 44, character 21). *Sisicottus panopeus* can also be distinguished from *S. crossoclavis*, *S. cynthiae*, *S. orites*, *S. nesides*, and *S. aenigmaticus* by the form of the dorsal fold of the dorsal plate which is membranous in *S. panopeus* (cf. Fig. 65, character 24) instead of sclerotized (Fig. 71).

Description.—Medium-sized (carapace

length = 0.67–0.96 mm); coloration typical (see description section for *Sisicottus*). Distal suprategular apophysis of male palpus moderately sclerotized, of moderate length, extends about half way down ectal side of palpal bulb; rounded on inside margin; terminal margin about level with suprategular membrane (Figs. 40, 45). Palpal tibia moderately long with a long apophysis; ectal tibial process absent (Fig. 41); dense cluster of macrosetae (7–11) on ectal side of palpal tibia. Females with ventral plate invagination shallow to absent (Figs. 43, 51). Posterior face of dorsal plate subrectangular with flat ventral margin (Figs. 44, 52). Dorsal fold of dorsal plate membranous. Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts sinuous (cf. Fig. 65). Internal structure of epigynum virtually identical to that of *S. montanus* (Fig. 65). See Tables 2–4.

Natural history.—*Sisicottus panopeus* and *S. nesides* were found in the same vial or identically labeled vials several times during this study. Crawford & Edwards (1988) observed that in Washington these two species occupy distinct ecological niches, with *S. panopeus* apparently restricted to alpine and subalpine habitats and *S. nesides* more common at lower elevations. These two species are syntopic, however, where their ecological ranges overlap at or just below the tree line. *Sisicottus panopeus* has also been collected syntopically

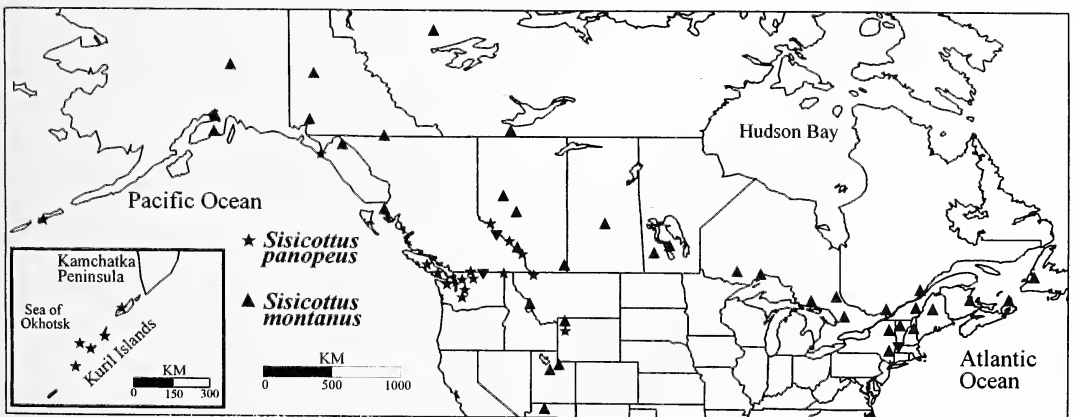


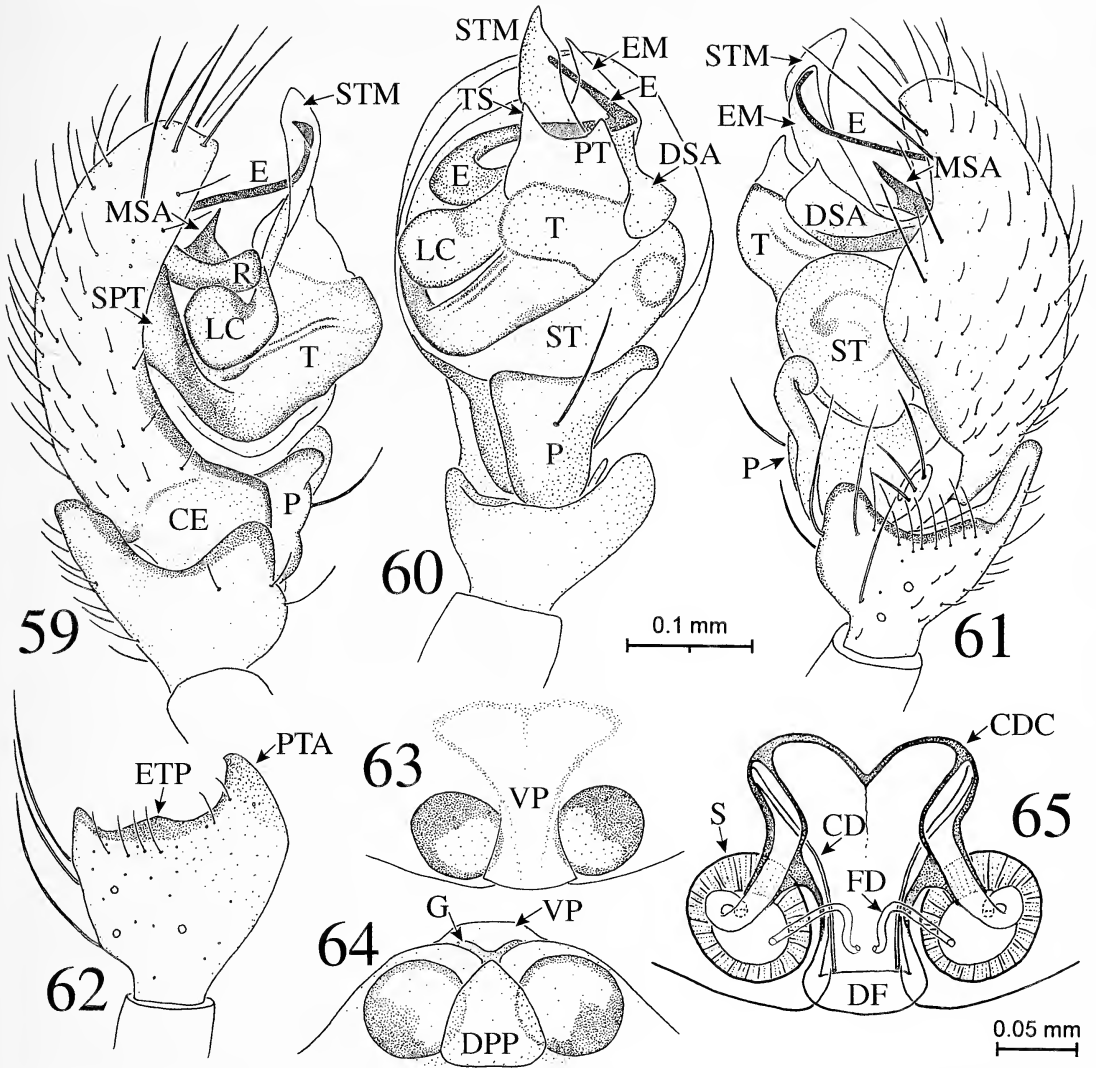
Figure 58.—North America with inset of the Kuril Islands, showing distribution of *Sisicottus panopeus* (★) and *S. montanus* (▲).

with *S. montanus*, *S. crossoclavis*, and *S. orites*. Collection labels indicate that this species may be found in moss, bogs, meadows, and forests, especially those with a conifer component. However, *Sisicottus panopeus* from the Kuril Islands occur in an ecological niche that is unusual for *Sisicottus* since many of the records come from islands that are completely unforested and occasionally devoid of even shrub vegetation (R. Crawford pers. comm.).

Distribution.—Wyoming, Montana, Washington, Alberta, British Columbia and Alaska. Recent collections of this species from the Kuril Islands (between Japan and the Kamchatka Peninsula) make it the only *Sisicottus* species known from Asia (Fig. 58). Further collections in Asia may well yield additional records of *S. panopeus*.

Material examined.—**CANADA:** *Alberta:* Bow Lake, Banff Nat'l Park, elev. 6400 feet, moss and willow litter nr lake, 9 August 1973, 1 ♀ (E.E. Lindquist, CNC); Bow Pass, 64 mi. NW Banff, Berlese spruce duff, 12 October 1953, 1 ♂ 2 ♀ (O. Peck, CNC); Cathedral Prov. Park, Pyramid L. Trail, 5–9 July 1986, 1 ♂ 1 ♀ (S.G. Cannings, CNC); Mt. Edith, Cavill Lodge, 52°41'N, 118°09'W, 24 August 1965, 1 ♀ (J. & W. Ivie, AMNH); Highwood Pass, 35 mi. S Kananaskis, ex spruce-larch litter, 28 July 1970, 1 ♀ (E.E. Lindquist, CNC); Kananaskis P.P., Mt. Indefatigable, lichens on stones in lodgepole pine forest at base of mountain, 20 July 1983, 2 ♂ 1 ♀ (V. Behan, CNC); Lake Louise, 4 August 1927, 3 ♂ (Crosby, AMNH); Marmot Cr., 13 mi. SW Kananaskis F.E.S., 6000 feet, ex damp moss cover on forest floor, 20 August 1970, 1 ♂ 1 ♀ (E.E. Lindquist, CNC); Cameron Lake, Waterton Lakes Nat'l Park, interception trap, 4–17 July 1980, 2 ♂ 4 ♀ (H.J. Teskey, CNC), Crandell L. trail, mossy area on N. slope in mixed woods, 13 June 1980, 3 ♀ (I.M. Smith, CNC), Rowe Lake Trail, 6300 feet, sifting moss, edge of stream, 7 June 1980, 5 ♀ (J.M. Campbell, CNC). *British Columbia:* Manning Prov. Pk., Skyline Trail, 1768 m, *Phyllodose*, *Kalmia*, moss, lichen, 12 July 1986, 3 ♀ (V. Behan, CNC); Nitinat, Heather Mtn., V.I., ca. 3600 feet, moss on seepage slope, 14 July 1979, 3 ♀ (I.M. Smith, CNC), moss at cold seepage area, 27 July 1979, 4 ♀ (I.M. Smith, CNC); Strathcona Park, Vancouver Is., Cream Lake, 1260 m, moss litter, 18 August 1988, 2 ♀ (C. Guppy, CNC); Yoho Glacier, 5 August 1914, 1 ♂ 1 ♀ (Emerton, AMNH); Yoho Glacier Camp, 5 August 1914, 6 ♂ 7 ♀ (Emerton, MCZ). **RUSSIA:** *Kuril Islands:* Ekarma Island, E side Cape Shpileroi, 4 m, 48.958°N, 153.920°E, in grass litter of beach meadow, 10 August 1996, 1 ♂ 6 ♀ (T.W. Pietsch, UWBM); Kharimotan Island, Inland from Severgina Bay, 15 m, 49.159°N, 154.478°E, ex sphagnum

and other mosses around dry interdune wetlands, 8 August 1996, 5 ♀ (R. Crawford, UWBM); Matua Island, army base, east end of island, 25 m, 48.068°N, 153.257°E, ex alder and grass litter in thickets of *Alnus maximowiczii*, 14 August 1996, 1 ♂ 5 ♀ (R. Crawford, UWBM); Ohirinkotan Island, E side Cape Pichy, NW corner of island, 15 m, 48.986°N, 153.472°E, litter of tall grass meadow on steep slope -treeless, 10 August 1996, 5 ♀ (T.W. Pietsch, UWBM); Onekotan Island, slope above Trundi River, 90 m, 49.280°N, 154.749°E, ex alder thicket litter in coastal slope meadow, 9 August 1996, 2 ♂ 2 ♀ (R.L. Crawford, T. Pearce, UWBM); Onekotan Island, 2 km S of Cape Subbotyna -river valley, 49.396°N, 154.646°E, ex herbaceous litter in river valley, 5 August 1996, 2 ♀ (T. Pearce, UWBM); Paramushir Island, SW shore, Sholikhova Bay, 50°22'N, 155°37'E, 13–25 August 1996, 1 ♂ (Y. Marusik, UWBM); Shishkotan Island, Zakatnaya Bay, 20 m, 48.778°N, 54.036°E, ravine in coastal slope meadow ex litter *Alnus maximowiczii*, *Sorbus samburifolia*, 11 August 1996, 5 ♂ 17 ♀ (R. Crawford, UWBM); Ushishir Island, Kraternaya Bay (central peninsula), 5–20 m, 47.510°N, 152.815°E, ex litter of Petasites patch in north exposed steep grass meadow, 20 August 1995, 2 ♂ 3 ♀ (Y. Marusik, UWBM). **UNITED STATES:** *Alaska:* Aleutian Isl., Umnak, Fox Islands, July 1958, 4 ♂ 5 ♀ (C. Lindroth, MCZ); Lituya Bay, Glacier Bay National Monument, Mt. Blunt, subalpine, 58.630°N, 137.493°W, 2100 feet, sifted from moss in shrubland, 9 August 1979, 1 ♂ 1 ♀ (D.H. Mann, UWBM). *Montana:* Glacier National Park, Swiftcurrent Mountain, 7500 feet, 19 August 1953, 1 ♀ (Levi, MCZ); *Washington:* Clallam County, Olympic National Park, Waterhole Camp, 4975 feet, 47.944°N, 123.425°W, pitfalls in spring meadow, 30 July–8 August 1986, 11 ♂ 3 ♀ (R. Crawford, UWBM); Olympic Nat'l Park, Obstruction Peak, 5900–6000 feet, 3 August 1973, 3 ♂ 4 ♀ (A. Smetana, AMNH); King County, Source Lake 3760–3840 feet, 47.455°N, 121.451°W, under rock up slope from lake adjacent to snowfield, 2 August 1986, 1 ♂ (R. Crawford, UWBM); Okanogan County, Cold Spr Camp, 1850 m, 48.938°N, 119.789°W, ex rotten log, 3 August 1985, 1 ♂ 1 ♀ (R. Crawford, UWBM); Pend Oreille County, Deemer Creek, 4600 feet, 48.931°N, 117.089°W, sifted from willow litter in bog, 13 June 1986, 1 ♀ (R. Crawford, UWBM); Pierce County, Mt. Rainier National Park, Golden Gate 6400 feet, 46.799°N, 121.722°W, 2 pitfalls -heather and sedge meadow, 25 August–6 September 1975, 1 ♀ (D.H. Mann, UWBM); Paradise Camp, Mt. Rainier, 19 August 1927, 2 ♂ 6 ♀ (Crosby, 1927); Paradise, Mt. Rainier National Park, 46°48'N, 121°44'W, 12 September 1965, 10 ♂ 13 ♀ (J. & W. Ivie, AMNH); Pierce County, Bearhead Mtn., 6000–6089 feet, 47.023°N, 121.814°W, ex heather and under rock, 15 August 1982, 5 ♀ (R.



Figures 59–65.—*Sisicottus montanus*. 59–62, Palpus of male from Mt. Washington, New Hampshire. 59, Mesal view; 60, Ventral view; 61, Ectal view; 62, Palpal tibia, dorsal view. 63, 64, Epigynum of female from Mt. Washington, New Hampshire. 63, Ventral view; 64, Posterior view. 65, Cleared epigynum of female from near Soubunge Mountain, Piscataquis County, Maine, dorsal view. Scales: Fig. 65 = .05 mm; other figures = 0.1 mm.

Crawford, UWBM); Skagit County, Coney Pass, 3400 feet, 48.329–331°N, 121.736°W, swept -sub-alpine meadow, 27 July 1980, 1♂, (R. Crawford, UWBM); Skagit County, Dock Butte, 5000 feet, 48.640°N, 122.803°W, under rocks and wood, 13 September 1986, 6♂11♀ (R. Crawford, UWBM); Snohomish County, Box Mtn. Lake, 5050 feet, 48.223°N, 121.121–3°W, under wood on sand/mud shore, 5 August 1989, 2♀ (R. Crawford, UWBM). Wyoming: Grand Canyon, Yellowstone Park, 30 August 1927, 2♂ (Crosby, AMNH); Teton Park, Holly Lake, 9400 feet, 43°N, 110°W, 10 August 1950, 1♂5♀ (D.C. Lowrie, AMNH); Togwatee

Pass, 10,000 feet, 43°N, 110°W, 8 August 1950, 1♀ (D.C. Lowrie, AMNH).

Sisicottus montanus (Emerton 1882)

Figs. 47, 48, 53, 54, 57–65

Tmeticus montanus Emerton 1882: 55, fig. pl. xvi, fig. 3 [♂,♀]. Male lectotype from UNITED STATES: New Hampshire, Mt. Washington, 13 June 1877, J.H. Emerton, in MCZ, examined.

Erigone collina Marx 1890: 533, 538, 593 (*nomen novum*). Synonymy by Bishop & Crosby 1938.

Oedothorax montanus: Crosby 1905: 312; Petrunkevitch 1911: 264.

Gongylidium montanus: Emerton 1920: 315.

Sisicottus montanus: Bishop & Crosby 1938: 57–60, figs. 6–8 [♂ ♀]. Chamberlin & Ivie 1939, fig. 40 [♂]. Roewer 1942: 650. Bonnet 1958: 4065. Holm 1967: 61. Kaston 1981: 208–209, figs. 653–657 [♂, ♀]. West et al. 1984: 87. Koponen 1987: 281–283, 285. Crawford 1988: 15 (in part). Jennings et al. 1988: 61, 63. Aitchison-Benell & Dondale 1990: 224. Dondale et al. 1997: 89. Platnick 1993: 351 (after Crawford & Edwards 1988, misidentification); 1997: 427.

Diagnosis.—Males of *S. montanus* are distinguished from those of all other *Sisicottus* species by the form of the palpal tibia; the palpal tibial apophysis is tapered, ectally curved, and longer than that of *S. montigenus* and *S. quoylei* and the palpal tibia is shorter than that of *S. panopeus*, *S. crossoclavis*, *S. cynthiae*, *S. orites* and *S. nesides* (Figs. 57, 62, character 16). *Sisicottus montanus* males share with *S. panopeus* and *S. crossoclavis* a distal supratregular apophysis that extends about half way down the ectal side of the palpal bulb (Fig. 61, character 4); all other *Sisicottus* species have a distal supratregular apophysis that extends to near the ventral midline of the palpal bulb. *Sisicottus montanus* is distinguished from *S. panopeus* and *S. crossoclavis* by the presence of an ectal tibial process in *S. montanus* (Fig. 62, character 17). Also, the form of the distal supratregular apophysis is very different in these species. *Sisicottus crossoclavis* has a heavily sclerotized distal supratregular apophysis with a serrated terminal margin (Fig. 67, character 3). *Sisicottus montanus* and *S. panopeus* both have a moderately sclerotized distal supratregular apophysis (character 3) but in *S. montanus*, the distal supratregular apophysis projects ventrally past the level of the supratregular membrane (Fig. 61) while in *S. panopeus*, the distal supratregular apophysis projects at most only slightly beyond the level of the supratregular membrane (Fig. 40). *Sisicottus panopeus* and *S. crossoclavis* also have more macrosetae in their ectal tibial cluster (7–11 in *S. panopeus*; 7–9 in *S. crossoclavis*) than does *S. montanus* (2–6).

Females of *S. montanus*, like those of *S. panopeus*, *S. crossoclavis*, and *S. cynthiae*, have a shallow ventral plate invagination (Fig. 63, character 19); this separates them from fe-

males of *S. montigenus*, *S. quoylei*, *S. aenigmaticus*, *S. orites*, and *S. nesides*. *Sisicottus montanus* is unique among species with a shallow ventral plate invagination in having a groove formed by the enfolding of the ventral plate (Figs. 53, 54). *Sisicottus montanus* can also be distinguished from *S. panopeus* by the form of the posterior face of the dorsal plate which is pointed ventrally in *S. montanus* (Fig. 64, character 21) and is flat ventrally in *S. panopeus* (Fig. 44). *Sisicottus montanus* can also be distinguished from *S. crossoclavis*, *S. cynthiae*, *S. orites*, *S. nesides* and *S. aenigmaticus* by the form of the dorsal fold of the dorsal plate, which is membranous in *S. montanus* (Fig. 65, character 24) instead of sclerotized (Fig. 71).

Description.—Medium-sized (carapace length = 0.67–0.96 mm); coloration typical (see description section for *Sisicottus*). Distal supratregular apophysis of male palpus moderately sclerotized, of moderate length, extends about half way down ectal side of palpal bulb; rounded on inside margin; terminal margin ventral to level of supratregular membrane (Figs. 47, 61). Palpal tibia short with moderately short palpal tibial apophysis (Fig. 62); small ectal tibial process present; sparse cluster of macrosetae (2–6) on ectal side of palpal tibia. Females with ventral plate invagination shallow to absent (Figs. 53, 63). Posterior face of dorsal plate triangular, widest near its dorsal margin with sharply rounded or pointed ventral apex (Fig. 64). Ventral plate enfolding forming a groove (Figs. 53, 54). Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts sinuous (Fig. 65). See Tables 2–4.

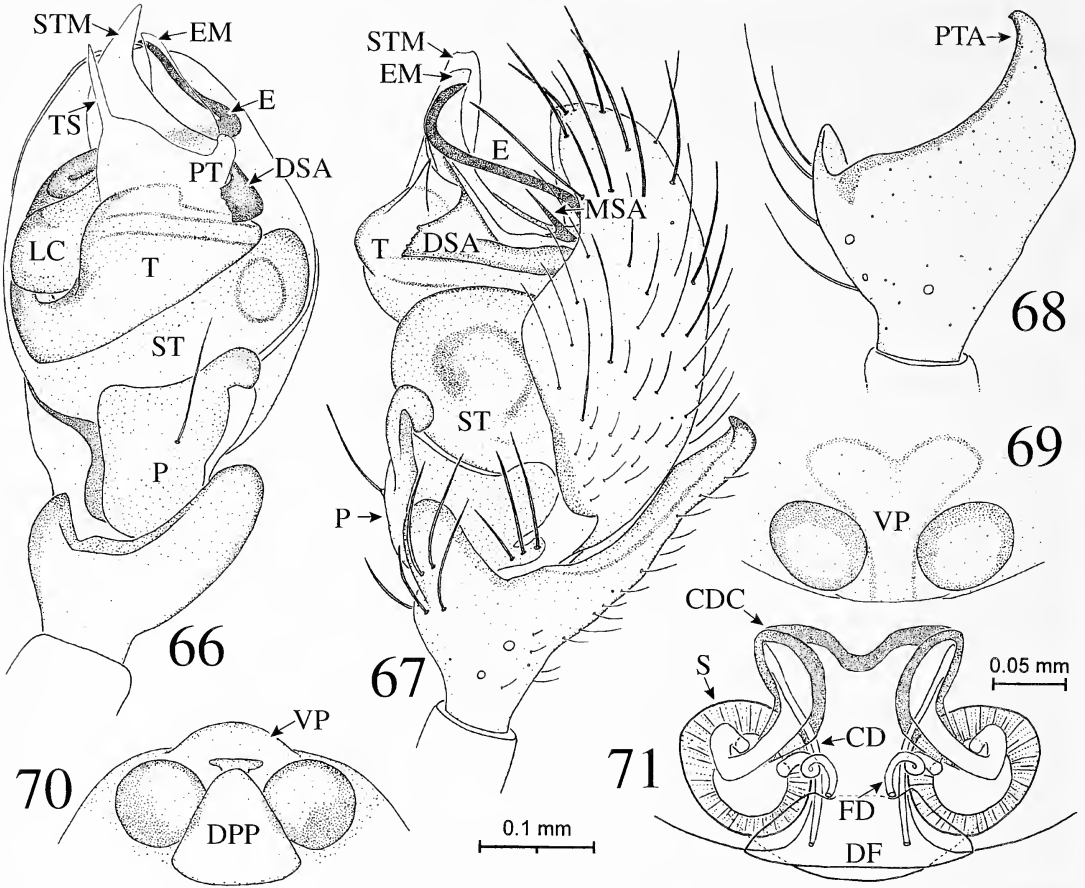
Natural history.—Aitchison-Benell & Dondale (1990) have reported that *S. montanus* in Manitoba may be found in boreal forest, bogs, ditches, mixed woods, leaf litter, moss and grass. Jennings et al. (1988) found that *S. montanus* in Maine preferred uncut spruce-fir forest habitats over clearcut strips. In a study of spiders living in ground habitats across an ecological/elevational gradient in Quebec, Koponen (1987) found *S. montanus* to be the dominant species in his collections from balsam fir forest at 850 m elevation. In this study, *S. montanus* was more rarely found in three other habitats: a mixed deciduous forest site

at 580 m elevation, a windy high elevation (920 m) scrub forest habitat near the tree line, and a somewhat sheltered summit below the tree line (870 m) with short birch and spruce trees. Collection labels record *S. montanus* from elevations of sea level to above tree line. This species is often associated with moss, bogs, and forest litter, especially from forests with a conifer component. It has been collected syntopically with *S. panopeus*, *S. orites*, and *S. nesides* and is also sympatric with *S. quoylei*.

Distribution.—Canada, New England, Alaska, Washington, and the Rocky Mountains region south to Arizona (Fig. 58).

Material examined.—**CANADA:** *Alberta:* Lake Louise, 4 August 1927, 3♂16♀ (Crosby, AMNH); Sulfur Mt., Banff, 2 August 1927, 1♂ (Crosby, AMNH); Lodgepole Pine Cpgd area, 1 mi. S Elkwater, Cypress Hills Prov. Pk., ex moist herbal mate substrate by seepage, 20–27 July 1978, 1♀, (E.E. Lindquist, CNC); House R. at Little Smoky River, 55°27'N, 117°10'W, 6 September 1968, 1♂3♀, (W. Ivie, AMNH); Jasper, 18 August 1914, 1♂ (Emerton, MCZ); White Court, 54°08'N, 115°41'W, 6 September 1968, 3♂7♀ (W. Ivie, AMNH). *British Columbia:* Metlakatla, 1♂1♀ (Emerton, AMNH); Summit Lake, pitfall in moss above tree line, 1 June–8 July 1981, 2♂1♀ (Dondale, CNC). *Manitoba:* R.M.N. Pk., Clear Lake, pan trap, beaver meadow, 8 June 1979, 1♂1♀ (S.J. Miller, CNC); Lake Audy, Riding Mtn. Nat'l Park, sifting grass and moss, 28 August 1979, 8♂17♀ (J. & M. Redner, CNC); nr. Wasagaming Riding Mtn. Nat'l P., in boggy area, 23 August 1979, 1♀ (J. & M. Redner, CNC). *New Brunswick:* Kouchibouguac N.P., forest edge on beach, 8 June 1977, 1♂ (S.J. Miller, CNC). *Newfoundland:* Corner Brook Lake, sifted from moss, 13 July 1984, 2♂1♀ (L. Hollett, CNC). *Northwest Territories:* Mackenzie, Alexandra Falls, Hay River, 60°30'N, 166°17'W, 16 August 1965, 1♀, (J. & W. Ivie, AMNH); Lac Maunoir, pitfall trap, 19–27 July 1969, 2♂4♀ (G.E. Shewell, CNC). *Nova Scotia:* Cape Breton Highlands National Park, MacKenzie Mtn., 300 m, ex malaise trough, 28 June–7 July 1983, 2♂1♀ (J.R. Vockeroth, CNC); Cape Breton Highlands National Park, 46°48'N, 60°41'W, 400 m, ex fen-pans, 8 June 1983, 1♂ (H. Goulet, CNC). *Ontario:* Bondi Village, Kuskoka District, moss in fir woods, 28 August 1975, 1♂2♀ (D. Maddison, CNC); English River (settlement), 49°13'N, 90°58'W, 24 July 1965, 2♀ (J. & W. Ivie, AMNH); Goward, 47°03'N, 79°55'W, 20 August 1952, 1♀ (C. Goodnight, AMNH); Nipigon, 48°N, 88°W, 12 August 1948, 1♀ (Gertsch & Kurata, AMNH). *Quebec:* Lac Cornu, Cté de Terrebonne, 3–4 September 1989, 1♀ (R. Hutchinson, CNC);

Parc des Grandes Jardins, Mont du Lac des Cygnes, 2 June–14 September 1985, 70♂45♀ (S. Koponen, UTZM); St. Méthode, nr. Lac St. Jean, litter, river bank, 13 July 1982, 1♂ (C. Dondale & J. Redner, CNC); Sherbrooke, sifting litter under trees, 20 September 1972, 2♂2♀ (Dondale & Redner, CNC). *Saskatchewan:* Prince Albert, 24 August 1914, 1♂ (Emerton, MCZ). *Yukon:* Alaska Hiway, Milepost 700, 60°05'N, 130°25'W, 2 September 1968, 1♂ (W. Ivie, AMNH); Dempster Hwy., km 220N, Tamarack Bog, ex *Alnus crispa*, *Picea mariana* litter, 26 June 1987, 1♀ (V. Behan, CNC); Kluane Lake, Kluane Nat'l Park, litter, 6 July 1981, 2♂2♀ (C.D. Dondale, CNC); North Fork Pass, 64°33'N, 138°15'W, sifting litter, 20 June 1981, 5♀ (C.D. Dondale, CNC). **UNITED STATES:** *Alaska:* Chatanika River Roadside Park, 65°08'N, 147°30'W, 17 August 1968, 1♂3♀ (W. Ivie, CNC); Trail to Denver Glacier, Skagway, 25 June 1936, 1♂ (Crosby, AMNH); Matanuska, 61°32'N, 149°12'W, September 1944, 1♀ (Chamberlin, AMNH), October 1943, 1♂ (J.C. Chamberlin, AMNH); Primrose Camp, 18 mi. N. of Seward, 60°20'N, 149°20'W, 24 August 1968, 15♂23♀ (W. Ivie, AMNH). *Arizona:* Kaibab For., 36°30'N, 112°30'W, 4 September 1931, 4♂4♀ (R.V. Chamberlin, AMNH). *Maine:* Piscataquis County: near Soubunge Mtn., pitfall coll., dense and striped spruce-fir forest, May, June, and July, 1977 and 1978, specimens in many vials, (D.T. Jennings, M.W. Houseweart, AMNH, CAS, CNC, USNM); Van Buren, 15 July 1914, 1♂ (Emerton, MCZ). *Massachusetts:* Berkshire County, Mt. Greylock, 3400 feet, decid. litter, 15 October 1990, 2♂1♀ (R.L. Edwards, USNM). *Montana:* Gird Creek, Ravalli County, 26 August 1934, 1♀ (W.L. Jellison, AMNH). *New Hampshire:* Coos County, Mt. Washington toll road, 0.3 mi. below halfway hse., 1100 m, Berl. litter, spruce-fir-birch forest, 15 October 1978, 1♂ (A. Newton, M. Thayer, MCZ); Mt. Washington, 13 June 1877, 3♀ paralectotypes, (J.H. Emerton, MCZ). *New York:* Catskill Mtn. Pk., North Mtn. Trail, ex litter under balsam fir, 1 August 1985, 1♀ (V. Behan, CNC); Mt. MacIntyre, Essex County, 1 July 1923, 1♀ (AMNH). *Utah:* Mirror Lake, Uintah Mountains, 40°43'N, 110°53'W, 28 July 1936, 4♂4♀ (W. Ivie, AMNH); west side Utah Lake, heron rookery, 27 May 1934, 4♀ (Ivie, AMNH). *Vermont:* Camels Hump, 7 September 1908, 2♂ (Emerton, MCZ); Mt. Mansfield, pitfall B fir forest, 26 May–15 June 1982, 85♂30♀ (C. Dondale, J. Redner, CNC); Stratton Mtn., 3000 feet, 4 July 1913, 1♂ (Emerton, MCZ). *Washington:* Okanogan County, Cold Spring Camp, 1850 m, ex rotten log, 48.938°N, 119.789°W, 3 August 1985, 1♂ (R. Crawford, UWBM). *Wyoming:* Bay Bridge, Yellowstone Lake, 11 August 1940, 8♂9♀ (W. Ivie, AMNH); Grand Canyon, Yellowstone Park, 30 August 1927, 1♂ (Crosby, AMNH).



Figures 66–71.—*Sisicottus crossoclavis*. 66–68, Palpus of holotype from Hayden Lake, Idaho. 66, Ventral view; 67, Ectal view; 68, Palpal tibia, dorsal view. 69, 70, Epigynum of female from Deemer Creek, Washington. 69, Ventral view; 70, Posterior view. 71, Cleared epigynum of female from Rabbit Creek, Washington, dorsal view. Scales: Fig. 71 = 0.05 mm; other figures = 0.1 mm.

Sisicottus crossoclavis new species

Figs. 49, 50, 55–57, 66–72

Sisicottus sp. #1: Crawford 1988: 15.

Types.—Male holotype with female para-

type from UNITED STATES: Idaho, Harrison Cr., E side Hayden Lake, 47°N, 116°W, 25 July 1959, F.C. Raney, deposited in AMNH.

Etymology.—Formed from the Greek word *krossos*, meaning tasseled, and *clavis*, a synonym for the suprategulum used by F.O. Pickard-Cambridge (H.D. Cameron pers. comm.).

Diagnosis.—The distal suprategular apophysis in males of *S. crossoclavis* is widened distally with a serrated terminal margin and is unique among *Sisicottus* (Fig. 67). Males of *S. crossoclavis* share with *S. cynthiae*, *S. orites*, and *S. nesides* a heavily sclerotized distal suprategular apophysis (character 3); all other *Sisicottus* species have either a moderately sclerotized or membranous distal suprategular apophysis. They share with *S. panopeus* and *S. montanus* a distal suprategular apophysis that extends about half way down the ectal

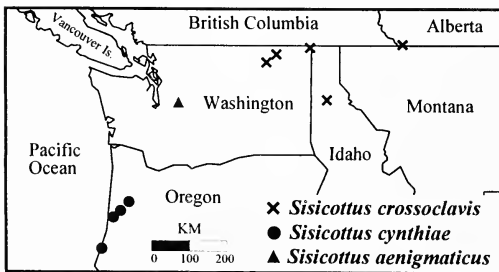


Figure 72.—Northwestern United States and southwestern Canada, showing distribution of *Sisicottus crossoclavis* (×), *S. cynthiae* (●), and *S. aenigmaticus* (▲).

side of the palpal bulb (Fig. 67, character 4); all other *Sisicottus* species have a distal suprategular apophysis that extends to near the ventral margin. They are distinguished from all other *Sisicottus* species except *S. panopeus* by the lack of an ectal tibial process (Fig. 68, character 17).

Females of *S. crossoclavis*, like those of *S. panopeus*, *S. montanus*, and *S. cynthiae*, have a shallow ventral plate invagination (Figs. 69, character 19); this separates them from females of *S. montigenus*, *S. quoylei*, *S. orites*, *S. nesides*, and *S. aenigmaticus*. *Sisicottus crossoclavis* is distinguished from *S. panopeus*, *S. montanus*, *S. montigenus*, and *S. quoylei* by the form of the dorsal fold of the dorsal plate which is sclerotized rather than membranous (character 24). *Sisicottus crossoclavis* is distinguished from *S. cynthiae* by the unusual form of the dorsal plate in *S. cynthiae*. In *S. cynthiae*, the posterior face of the dorsal plate has a ventral margin that is dorsal to the ventral extent of the spermathecae (Fig. 77); in all other *Sisicottus* species, including *S. crossoclavis*, the ventral margin of the posterior face of the dorsal plate is at about the level of the ventral extent of the spermathecae (Fig. 70).

Description.—Medium-sized (carapace length = 0.81–0.97 mm); coloration typical (see description section for *Sisicottus*). Distal suprategular apophysis of palpus heavily sclerotized, of moderate length, extends about half way down ectal side of palpal bulb; widened distally with serrated terminal margin (Fig. 67). Palpal tibia long with long, gradually curving palpal tibial apophysis; ectal tibial process absent (Fig. 75); dense cluster of macrosetae (7–9) on ectal side of palpal tibia. Females with ventral plate invagination shallow to absent (Figs. 55, 69). Posterior face of dorsal plate triangular with broadly rounded ventral margin (Figs. 56, 70). Dorsal fold of dorsal plate sclerotized (Fig. 71). Lateral margins of copulatory duct capsule in dorsal view sinuous with posterior tips of capsule oriented posteriorly; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts spiral (Fig. 71). See Tables 2–4.

Variation.—Of three known male specimens, two have a very long palpal tibial apophysis and palpal tibia, but a third specimen from Rabbit Creek, Washington has a palpal tibial apophysis and palpal tibia of

more moderate length (Fig. 57). Despite the difference in size, the tibias are similar in shape. Furthermore, all three specimens share virtually identical palpal bulbs and were found associated with indistinguishable females. I have concluded that both tibial morphotypes belong to a single species. The short tibia in the Rabbit Creek specimen may have been due unfavorable conditions during development or to some genetic condition.

Natural history.—*Sisicottus crossoclavis* has been collected from moss, rotting logs, and forest litter. Collection labels suggest that this species may have an affinity for relatively wet microhabitats.

Distribution.—Alberta, Idaho, and Washington (Fig. 72).

Material examined.—**CANADA:** *Alberta:* Waterton Lakes N.P., moss and litter on damp seepage rock face, 26 June 1980, 1♀ (I.M. Smith, CNC); **UNITED STATES:** *Washington:* Ferry County, S Fk. Boulder Cr., 2560 feet, 48.756°N, 118.249°W, *ex* cottonwood-cedar litter, 15 July 1989, 1♀ (R. Crawford, UWBM). Ferry County, Rabbit Creek, 3500 feet, 48.539°N, 118.605°W, *ex* alder litter; *ex* moss, logs, and ground in forest, 18 July 1989, 1♂5♀ (R. Crawford, UWBM). Pend Oreille County, Deemer Creek, 4600 feet, 48.931°N, 117.089°W, under rocks and logs; from pitfalls; in soggy moss at stream edge; web in soil depression; rotting log, 11–14 July 1986, 1♂6♀ (R. Crawford, UWBM); Spokane County, Mt. Spokane, 5000 feet, *ex* moss, herbs, nr. edge seepage area, 28 August 1985, 1♀ (C.C. Lindquist, CNC).

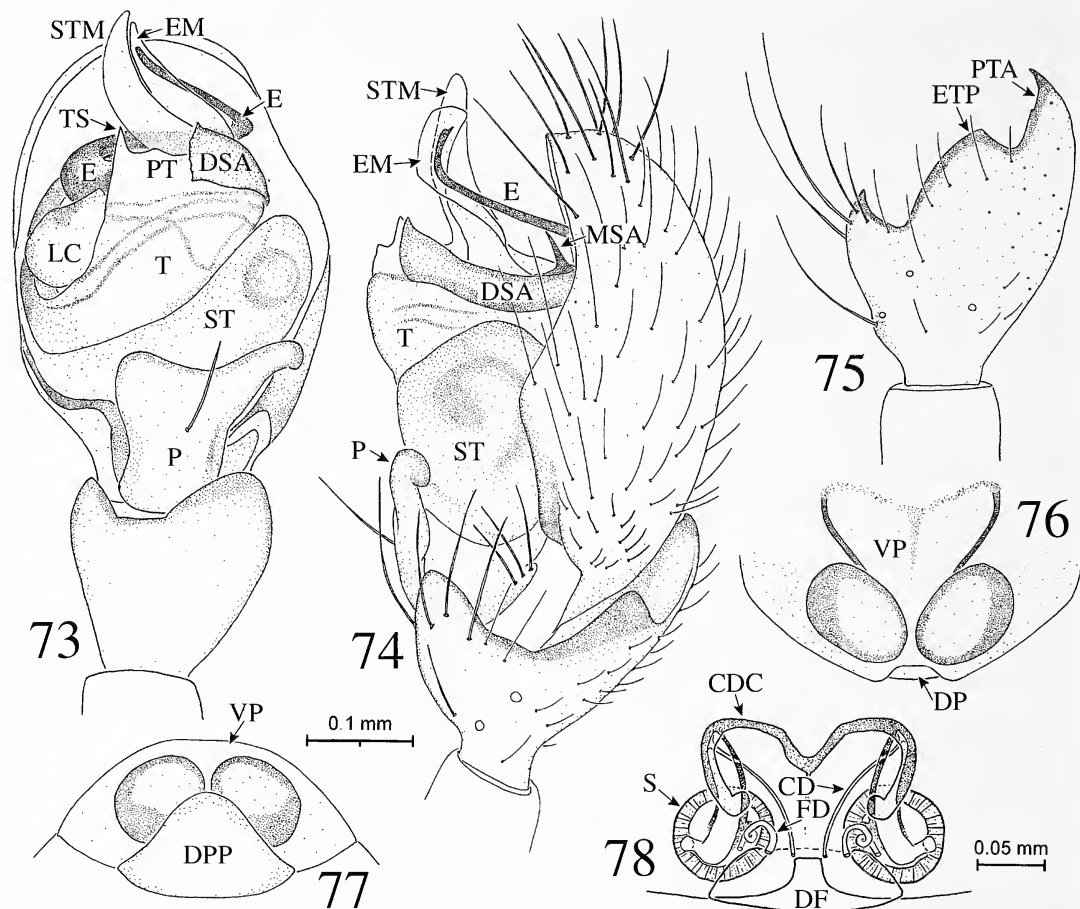
Sisicottus cynthiae new species

Figs. 72–80, 85, 86

Types.—Male holotype from UNITED STATES: Oregon, Benton County, Mary's Peak, 44°N, 123°W, 29 September 1960, J.D. Lattin, deposited in AMNH.

Etymology.—Named for my friend, Cynthia Zujko-Miller, whose support during the course of this project contributed substantially to its completion.

Diagnosis.—Males of *S. cynthiae* share with *S. crossoclavis*, *S. orites*, and *S. nesides* a heavily sclerotized distal suprategular apophysis (character 3); all other *Sisicottus* species have either a moderately sclerotized or membranous distal suprategular apophysis. They are distinguished from *S. crossoclavis* and *S. orites* by their much shorter palpal tibial apophysis (Fig. 75) and from *S. nesides* by

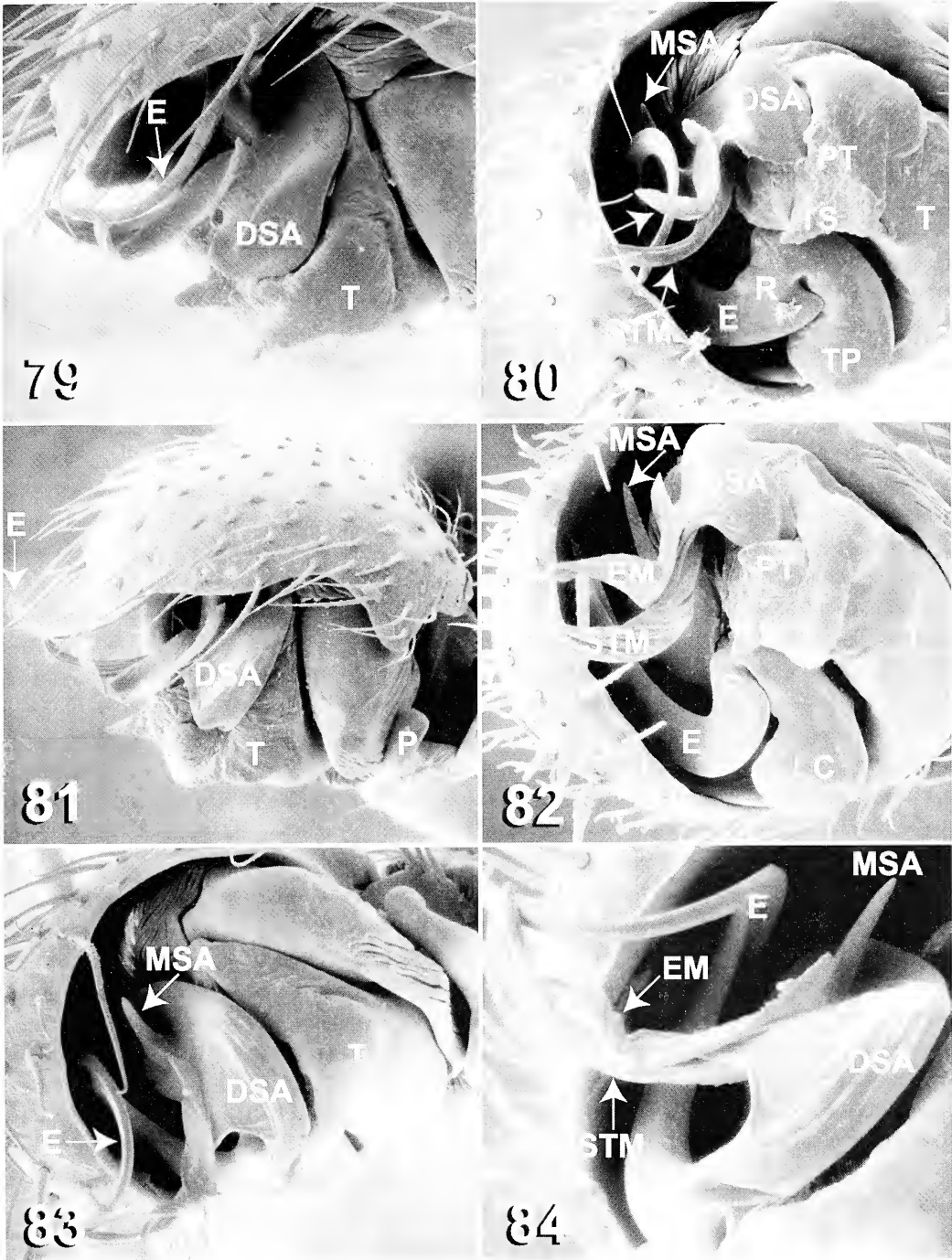


Figures 73–78.—*Sisicottus cynthiae*. 73–75, Palpus of holotype from Mary's Peak, Oregon. 73, Ventral view; 74, Ectal view; 75, Palpal tibia, dorsal view. 76, 77, Epigynum of female from Mary's Peak, Oregon. 76, Ventral view; 77, Posterior view. 78, Cleared epigynum of female from Grass Mountain, Oregon, dorsal view. Scales: Fig. 78 = 0.05 mm; other figures = 0.1 mm.

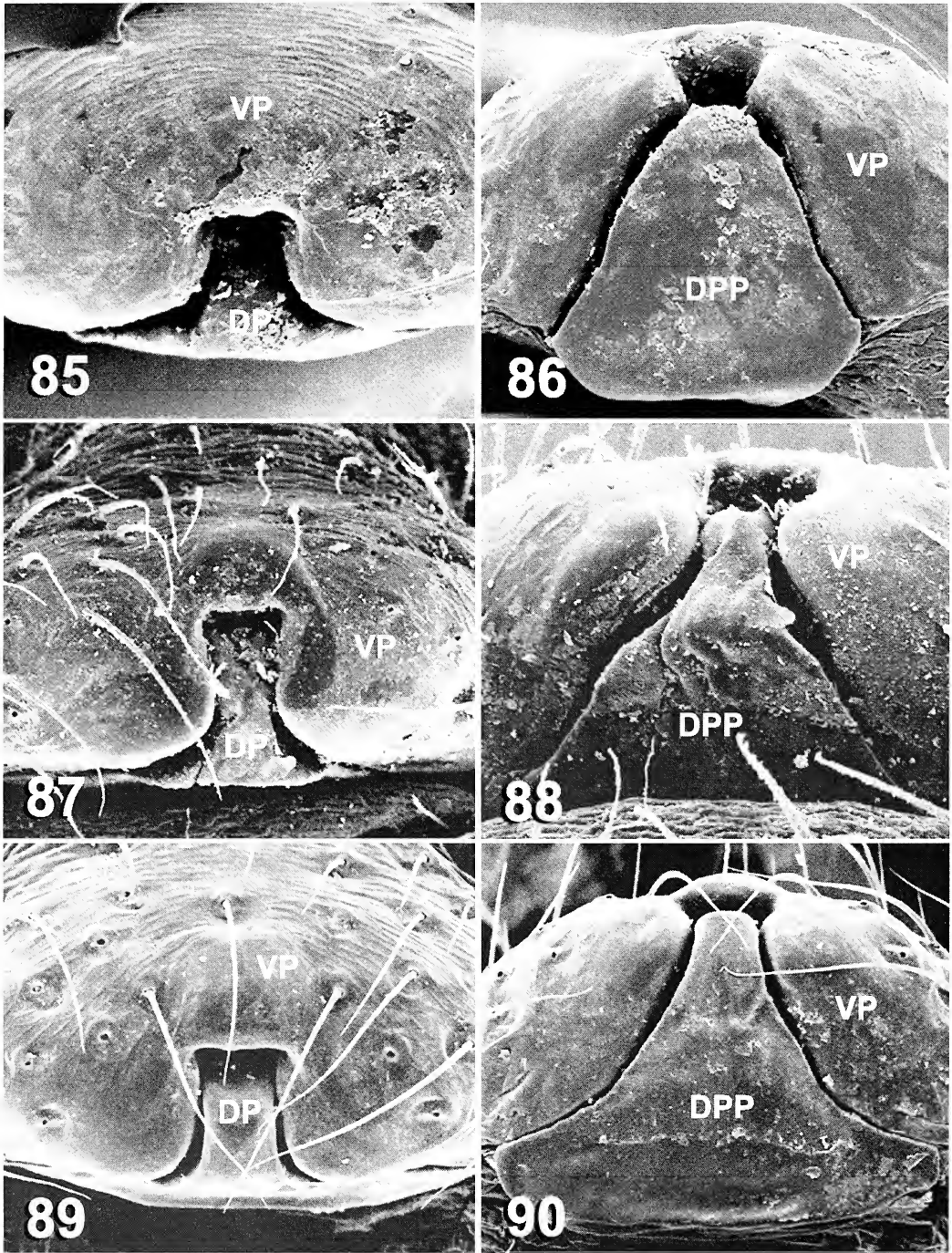
the terminus of the distal suprategular apophysis which has a broad, rippled ventral margin in *S. cynthiae* (Fig. 73). The corresponding region in *S. nesides* terminates in two apical points and is not widened distally (Fig. 102). The form of the ectal tibial process is unique in *S. cynthiae* being generally larger and more ectally placed than in other *Sisicottus* species (Fig. 75, character 17).

Females of *S. cynthiae* are distinguished from those of all other *Sisicottus* species by the form of the posterior face of the dorsal plate. In *S. cynthiae*, the posterior face of the dorsal plate has a ventral margin that is dorsal to the ventral extent of the spermathecae (Fig. 77); in all other *Sisicottus* species, the ventral margin of the posterior face of the dorsal plate is at about the level of the ventral extent of

the spermathecae (Fig. 70). *Sisicottus cynthiae*, like *S. panopeus*, *S. montanus*, and *S. crossoclavis*, have a shallow ventral plate invagination (Figs. 76, character 19); this separates them from females of *S. montigenus*, *S. quoylei*, *S. orites*, *S. nesides*, and *S. aenigmaticus*. *Sisicottus cynthiae* is distinguished from *S. panopeus*, *S. montanus*, and *S. crossoclavis* by the orientation of the posterior part of the copulatory duct capsule (character 32). In *S. cynthiae*, the posterior tips of the capsule are oriented mesally (Fig. 78). In *S. panopeus*, *S. montanus*, and *S. crossoclavis*, the posterior tips of the capsule are oriented posteriorly (Fig. 65). *Sisicottus cynthiae* is distinguished from *S. panopeus*, *S. montanus*, *S. montigenus*, and *S. quoylei* by the form of the dorsal fold of the dorsal plate which is sclerotized



Figures 79–84.—Scanning electron micrographs of *Sisicottus* palpi. 79, 80, *S. cynthiae* from Mary’s Peak, Oregon. 79, Ectal view; 80, Ventral view. 81, 82, *S. orites* from Mirror Lake, Utah. 81, Ectal view; 82, Ventral view. 83, 84, *S. nesides* from Primrose Camp, Alaska. 83, Ectoventral view; 84, Ventral view detailing distal supratregular apophysis.



Figures 85–90.—Scanning electron micrographs of *Sisicottus* epigyna. 85, 86, *S. cynthiae* from Charleston, Oregon. 85, Ventral view; 86, Posterior view. 87, 88, *S. orites* from Smith and Morehouse Canyon, Utah. 87, Ventral view; 88, Posterior view. 89, 90, *S. nesides* from Change Creek, King County, Washington. 89, Ventral view; 90, Posterior view.

rather than membranous (Fig. 78, character 24).

Description.—Large (carapace length = 0.88–1.10 mm); coloration typical (see description section for *Sisicottus*). Distal supratregular apophysis of male palpus heavily sclerotized, long, extends to near ventral midline of palpal bulb; slightly widened near terminal margin, which has rippled appearance (Figs. 73, 80). Palpal tibia long with medium sized apophysis; ectal tibial process pronounced (Fig. 75); moderately dense cluster of macrosetae (6–8) on ectal side of palpal tibia. Female with shallow ventral plate invagination (Figs. 76, 85). Posterior face of dorsal plate triangular with broadly rounded ventral margin located dorsal to ventral extent of spermathecae (Fig. 77). Lateral margins of copulatory duct capsule in dorsal view sinuous with tips of capsule oriented mesally toward each other; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts looped (Fig. 78). See Tables 2–4.

Natural history.—One collection label states that *S. cynthiae* has been collected from moss and another indicates that a female specimen was found in the stomach of a salamander. *Sisicottus cynthiae* is syntopic with *S. nesides*.

Distribution.—Oregon (Fig. 72).

Material examined.—UNITED STATES:

Oregon: Benton County, Mary's Peak, 44°N, 123°W, 29 September 1960, 4♂1♀ (J.D. Lattin, AMNH); Benton County, Grass Mountain, 44°N, 123°W, 30 October 1960, 4♂4♀ (J.D. Lattin, AMNH); Benton County, McGlynn Dr. ravine, moss on road bank, 23 January 1977, 1♂ (L. Russell, CNC); Charleston, 43°20'N, 124°20'W, 7 August 1947, 1♂5♀ (I.M. Newell, AMNH), July 1947, 1♂2♀ (I.M. Newell, AMNH); Lane County, Klickitat Mtn., N side, 23 January 1977, 2♀ (L. Russell, CNC); 10 mi. N of Philomath (*ex newt*), 44°40'N, 123°22'W, about 1950, 1♀ (R. Freiburg, AMNH).

Sisicottus orites (Chamberlin 1919)

Figs. 81, 82, 87, 88, 91–101

Grammonota orites Chamberlin 1919: 249 [♂, ♀].

Male holotype from UNITED STATES: Utah, Chalk Creek, Chamberlin, in MCZ, examined.

Oedothorax pidacitis Crosby & Bishop 1927: 151 [♂]. Male holotype from UNITED STATES: Colorado, Larimer County, Pingree Park, Stormy Peaks, 10,000 feet, 20 August 1924, Crosby, in

AMNH, examined. Synonymy by Chamberlin & Ivie 1933.

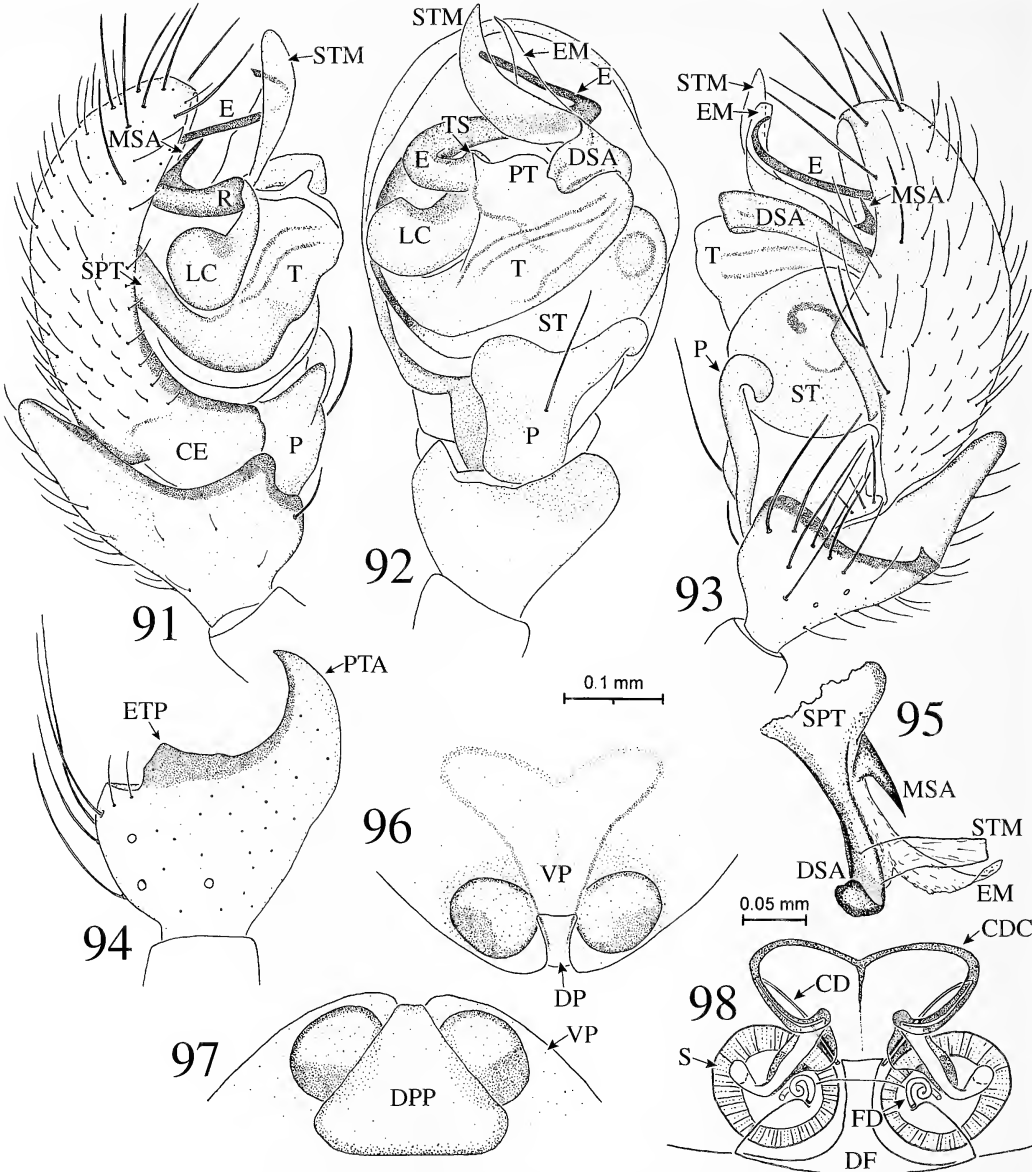
Oedothorax orites: Chamberlin & Ivie 1933: 22 [♀].

Sisicottus montanus, in part: Bishop & Crosby 1938: 57–60, fig. 5 [♂].

Sisicottus orites: Chamberlin & Ivie 1939: fig. 38 [♂]. Platnick 1993: 351.

Diagnosis.—Males of *S. orites* share with *S. crossoclavis*, *S. cynthiae*, and *S. nesides* a heavily sclerotized distal supratregular apophysis (character 3); all other *Sisicottus* species have either a moderately sclerotized or membranous distal supratregular apophysis. They are distinguished from *S. cynthiae* by their longer palpal tibial apophysis (Fig. 94). They are distinguished from *S. crossoclavis* by the presence of an ectal tibial process (Fig. 94, character 17), a long distal supratregular apophysis that extends to near the ventral midline of the palpal bulb, and a smooth terminal margin of the distal supratregular apophysis (Fig. 92, character 4). They are distinguished from *S. nesides* by the terminus of the distal supratregular apophysis which is rounded, often with a shallow central concavity (Fig. 92); in *S. nesides*, the terminus is bifurcated with the inside lobe coming to a sharp apex on or outside of the median line of the distal supratregular apophysis and the outside lobe coming to its apex on the outer margin (Fig. 102). Dimensions of the palpal tibia (Fig. 99) and the number of macrosetae in the ectal tibial cluster (8–13 in *S. orites*; 7–10 in *S. nesides*) may also be useful for distinguishing *S. orites* from *S. nesides*.

Females of *S. orites*, *S. nesides*, and *S. aenigmaticus* differ from those of all other *Sisicottus* species by the form of the copulatory duct capsule in dorsal view which has strongly bowed lateral margins (Fig. 98, character 31); in all other *Sisicottus* species, the lateral margins are sinuous to moderately bowed. Unlike *S. panopeus*, *S. montanus*, *S. crossoclavis*, and *S. cynthiae*, these species have a deep ventral plate invagination (Fig. 96, character 19). *Sisicottus orites* is distinguished from *S. aenigmaticus* by the width of the ventral plate invagination and by the form of the posterior face of the dorsal plate which is trapezoidal with concave sides in *S. aenigmaticus* (Fig. 107) and triangular with nearly straight sides in *S. orites* (Fig. 97, characters 21, 22). Females of *S. orites* are difficult to

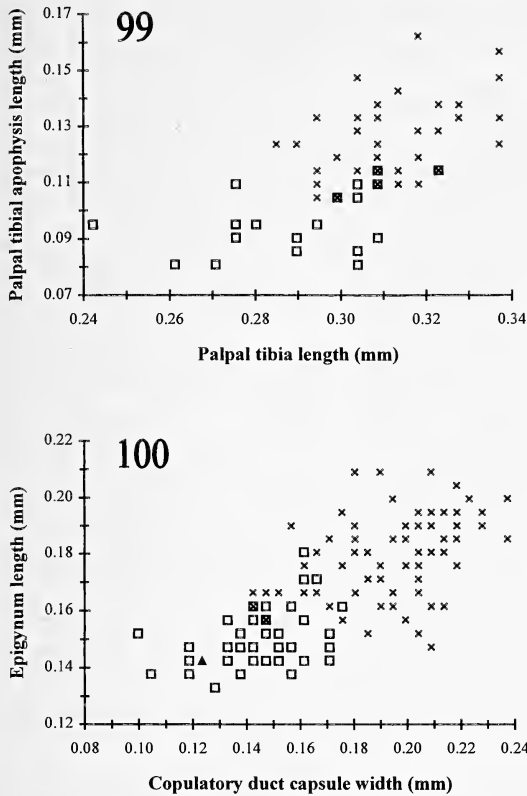


Figures 91–98.—*Sisicottus orites*. 91–94, Palpus of male from Mirror Lake, Utah. 91, Mesal view; 92, Ventral view; 93, Ectal view; 94, Palpal tibia, dorsal view. 95, Supratégulum separated from palpus of male from Smith and Morehouse Canyon, Utah, ectal view. 96, 97, Epigynum of female from Mirror Lake, Utah. 96, Ventral view; 97, Posterior view. 98, Cleared epigynum of female from Smith and Morehouse Canyon, Utah, dorsal view. Scales: Figs. 95, 98 = 0.05 mm; other figures = 0.1 mm.

distinguish from those of *S. nesides*. *Sisicottus nesides*, like *S. aenigmaticus*, have a dorsal plate with concave sides on its posterior face (character 22). Also, epigynum length and copulatory duct capsule width are both usually larger in *S. orites* than in either *S. nesides* or *S. aenigmaticus* (Fig. 100).

Description.—Large (carapace length =

0.88–0.20 mm); coloration typical (see description section for *Sisicottus*). Distal supra-
tegular apophysis of male palpus heavily
sclerotized, long, extends to near ventral mid-
line of palpal bulb; terminal margin rounded
or with shallow concave invagination (Figs.
82, 92). Palpal tibia long with long apophysis;
ectal tibial process present (Fig. 94); very



Figures 99–100.—Scattergrams of morphometric characters for males and females of *Sisicottus orites* (×) and *S. nesides* (□) and female of *S. aenigmaticus* (▲). 99, Palpal tibial apophysis length plotted against palpal tibia length in males; 100, Epigynum length plotted against copulatory duct capsule width in females.

dense cluster of macrosetae (8–13) on ectal side of palpal tibia. Females with deep ventral plate invagination (Figs. 87, 96). Posterior face of dorsal plate triangular with nearly straight sides (Figs. 88, 97). Dorsal fold of dorsal plate sclerotized (Fig. 98). Lateral margins of copulatory duct capsule in dorsal view strongly bowed with tips of capsule oriented mesally toward each other; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts looped (Fig. 98). See Table 2–4.

Natural history.—Collection labels indicate that this species is associated with wet moss and similar microhabitats. It has been collected syntopically with *S. montanus*, *S. panopeus*, and *S. nesides*.

Distribution.—From California, Utah, and

New Mexico north to Washington and Alberta (Fig. 101).

Material examined.—**CANADA:** *Alberta:* Waterton Lakes Nat'l Park, Cameron Lake, 5300–5500 feet, 9–19 June 1980, 8♂2♀ (J.M. Campbell, CNC), Lower Bertha Falls, sifted moss, 10 June 1980, 1♀ (J.M. Campbell, CNC); Lake Louise, 4 August 1927, 1♂4♀ (Crosby, AMNH); Mt. Edith, Cavill Lodge, 52°41'N, 118°09'W, 24 August 1965, 10♀ (J. & W. Ivie, AMNH); Whitemud Creek, Edmonton, soil sample, 8 May 1959, 3♀ (L.K. Smith, CNC). **UNITED STATES:** *California:* Laguna Lake, Laguna Canyon, 33°36'N, 117°45'W, 6 July 1934, 1♀ (Ivie & Rasmussen, AMNH). *Colorado:* Berthoud Pass, 39°58'N, 105°48'W, 24 August 1935, 1♂4♀ (Ivie, AMNH); Cameron Pass, 11,000 feet, 40°31'N, 105°52'W, 3 August 1946, 1♀ (C.C. Hoff, AMNH); Miguel County, Trout Lk., NE of Lizard Head Pass, San Juan Mtns., 3100 m, mud flats, moist sedges, 20 July 1959, 1♀ (H.W. Levi, MCZ); Pikes Peak, 11,600 feet, 38°52'N, 105°5'W, 22 July 1940, 3♀ (Ivie, AMNH). *Idaho:* 2 miles south of Tamarack, 44°56'N, 116°23'W, 17 October 1944, 2♂2♀ (Ivie, AMNH); Targhee Pass, 44°38'N, 111°18'W, 30 June 1962, 2♀ (Ivie, AMNH); Willow Flat camp, Franklin County, 42°N, 111°W, 5 July 1952, 3♀ (B. Malkin, AMNH). *Nevada:* Ruby Valley, 40°15'N, 115°25'W, September 1937, 2♂5♀ (Chamberlin, AMNH); White Pine County, Schell Mtns., Timber Cr. Cpgd. area, 30 mi. NE Ely, 8700 feet, from wet moss and substrate, 27 June 1989, 1♀ (E.E. Lindquist, CNC); White Pine County, Schell Mtns., 15 mi SE Ely, 7500 feet, wet moss-stream edge, 26 June 1989, 1♀ (E.E. Lindquist, CNC). *New Mexico:* Panchuela Cpgd, 18 mi. N Pecos, 8400 feet, *ex* liverwort carpet on moist rock wall, 28 August 1973, 1♂ (E.E. Lindquist, CNC). *Oregon:* Douglas County, Diamond Lake, 43°10'N, 122°08'W, 7 September 1949, 1♀ (V. Roth, AMNH); Grant County, Strawberry Creek Falls, 6800 feet, *ex* moss on rocks in falls spray zone, 23 July 1985, 1♀ (E.E. Lindquist, CNC); Grant County, Strawberry Lake area, 6400 feet, *ex* moss, herbs, rotting wood in seepage, 23 August 1985, 1♂ (E.E. Lindquist, CNC); Langdon Lake, Blue Mts, 13 September 1949, 4♀ (V. Roth, AMNH). *Utah:* nr Alta, Little Cottonwood Canyon, under stones in creek, 25 June 1985, 2♀ (C. Dondale & J. Redner, CNC); City Creek Can., Rotary Park, 46°48'N, 111°46'W, 11 September 1942, 8♂8♀ (Ivie, AMNH), 16 September 1942, 4♂4♀ (Ivie, AMNH); Logan Canyon, 4♀ (Chamberlin, MCZ); Mirror Lake, Uintah Mountains, 40°43'N, 110°53'W, 22 September 1932, 4♂4♀ (Ivie, AMNH), 28 July 1936, 4♂4♀ (Ivie, AMNH), 18 August 1942, 4♂4♀ (Ivie, AMNH); Smith and Morehouse Canyon, 40°47'N, 110°6'W, 7 October 1932, 4♂4♀ (W. Ivie, USNM); So. Fork Raft Riv., 8 mi. So. Lynn, 41°53'N,

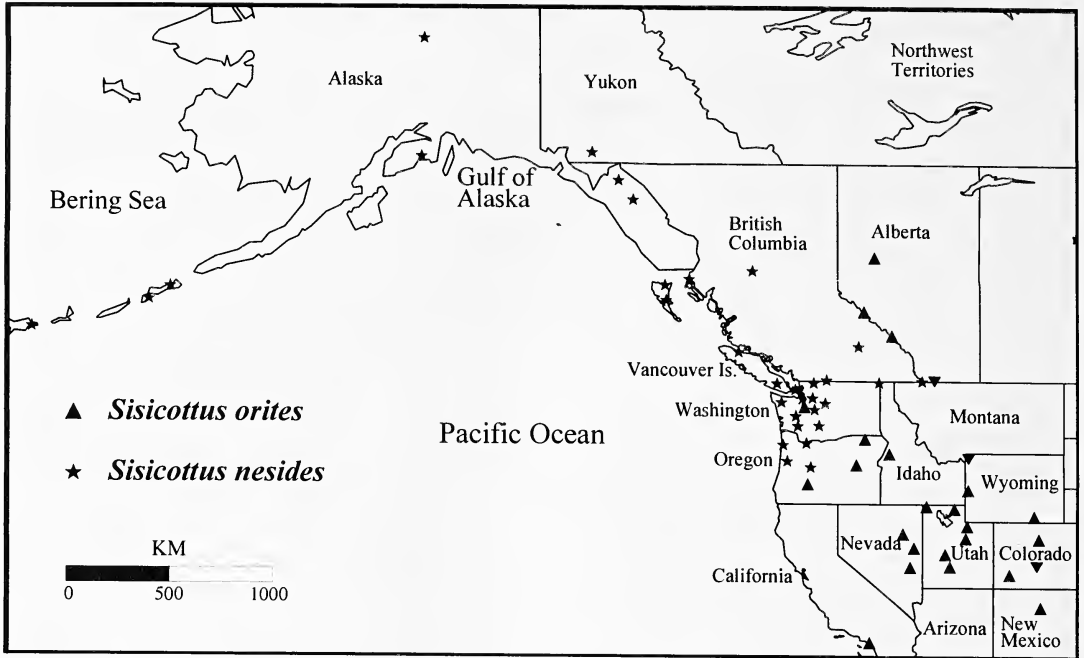


Figure 101.—Western North America, showing distribution of *Sisicottus orites* (▲) and *S. nesides* (*).

113°45'W, 6 September 1932, 5♂ 10♀ (Chamberlin & Ivie, AMNH); Vicinity of Salt Lake City, quad 40°N, 111°W, misc. 1928–1936, 4♂ 12♀ (AMNH). *Washington*: Seattle, 47°35'N, 122°20'W, May 1952, 1♂ 1♀ (Borys Malkin, AMNH). *Wyoming*: Canyon east of Bedford, 42°50'N, 110°50'W, 27 June 1962, 2♀ (Ivie, AMNH); Centennial, Wyoming University, 9500 feet, under log, 17 August 1936, 1♂ (AMNH).

Sisicottus nesides (Chamberlin 1921)

Figs. 83, 84, 89, 90, 99–105

Oedothorax nesides Chamberlin 1921: 36, plate III, figs. 1–2 [♂]. Male holotype from UNITED STATES: Alaska, St. Paul Island, 1910, H. Heath, in MCZ, examined.

Sisicottus montanus: Bishop & Crosby 1938: 57–60, fig. 4 [♂] (in part). Bragg & Leech 1972: 69 (misidentification).

Sisicottus nesides: Chamberlin & Ivie 1939: fig. 39 [♂]. Crawford & Edwards 1988: 437; figs. 23–24 [♀]. Platnick 1993: 351. Dondale et al. 1997: 89.

Sisicottus montanus nesides: Holm 1960: 124. Elevated by Crawford & Edwards 1988.

Sisicottus orites: West et al. 1984: 87 (misidentification).

Diagnosis.—Males of *S. nesides* share with *S. crossoclavis*, *S. cynthiae*, and *S. orites* a heavily sclerotized distal supratergular apophysis

(character 3); all other *Sisicottus* species have either a moderately sclerotized or membranous distal supratergular apophysis. They are distinguished from *S. crossoclavis* by the presence of an ectal tibial process (Fig. 103, character 17) and a long distal supratergular apophysis that extends to near the ventral midline of the palpal bulb and lacks a serrated terminal margin (Fig. 102, character 4); the distal supratergular apophysis in *S. crossoclavis* extends only about half way down the ectal face of the palpal bulb and has a serrated terminal margin (Fig. 67). *Sisicottus nesides* can be distinguished from other *Sisicottus* species with a long, heavily sclerotized distal supratergular apophysis by the terminus of the distal supratergular apophysis which is bifurcated with the inside apex coming to a sharp point on or outside of the median line and the outside apex coming to a point on the outer margin; this condition is unique among *Sisicottus* (Figs. 84, 102). The distal supratergular apophysis in *S. cynthiae* has a rippled terminal margin (Fig. 73); the distal supratergular apophysis in *S. orites* has a rounded terminal margin, often with a shallow central concavity (Fig. 92). Dimensions of the palpal tibia (Fig. 99) and the number of macrosetae in the ectal tib-

ial cluster (7–10 in *S. nesides*; 8–13 in *S. orites*) may also be useful for distinguishing *S. nesides* from *S. orites*.

Females of *S. nesides*, *S. orites*, and *S. aenigmaticus* differ from those of all other *Sisicottus* species by the form of the copulatory duct capsule in dorsal view which has strongly bowed lateral margins (*cf.* Fig. 98, character 31); in all other species, the lateral margins are sinuous to moderately bowed. Unlike *S. panopeus*, *S. montanus*, *S. crossoclavis*, and *S. cynthiae*, these species have a deep ventral plate invagination (Fig. 104, character 19). *Sisicottus nesides* is distinguished from *S. aenigmaticus* by the width of the ventral plate invagination and by the form of the posterior face of the dorsal plate which is trapezoidal in *S. aenigmaticus* (Fig. 107, character 21) and triangular in *S. nesides* (Fig. 105). Females of *S. nesides* are difficult to distinguish from those of *S. orites*. *Sisicottus nesides* have a dorsal plate with concave sides on the posterior face (Fig. 105, character 22) while the dorsal plate of *S. orites* has nearly straight sides on the posterior face (Fig. 97). Also, epigynum length and copulatory duct capsule width are both usually greater in *S. orites* than in either *S. nesides* or *S. aenigmaticus* (Fig. 100).

Description.—Large (carapace length = 0.88–1.20 mm); coloration typical (see description section for *Sisicottus*). Distal supra-regular apophysis heavily sclerotized, long, extends to near ventral midline; terminus bifurcated with longer inside apex coming to sharp point on or outside median line and the shorter outside apex coming to point on the outside margin (Figs. 84, 102). Palpal tibia moderately long with moderately long palpal tibial apophysis; ectal tibial process present (Fig. 103, character 17); dense cluster of macrosetae (7–9) on ectal side of palpal tibia. Females with deep ventral plate invagination (Figs. 89, 104). Posterior face of dorsal plate triangular with concave sides (Figs. 90, 105). Dorsal fold of dorsal plate sclerotized (*cf.* Fig. 98). Lateral margins of copulatory duct capsule in dorsal view strongly bowed with tips of capsule oriented mesally toward each other; fertilization ducts looped (*cf.* Fig. 98). Aside from some quantitative differences (Fig. 100), internal structure of epigynum virtually identical to that of *S. orites* (Fig. 98). See Tables 2–4.

Natural history.—This species has often been collected in moss and litter microhabitats in forests. In Washington, this species is partially separated from *S. panopeus* by ecological/elevational constraints (Crawford & Edwards 1988; also see the Natural History section in *S. panopeus*). *Sisicottus nesides* occurs syntopically with *S. montanus*, *S. cynthiae*, *S. aenigmaticus*, *S. crossoclavis*, and *S. orites*.

Distribution.—From Alaska, Alberta, British Columbia, Oregon, Washington, and the Yukon (Fig. 101). A published record from Nebraska is almost certainly erroneous (Rapp 1980 pers. comm.). A male and a female specimen from Lincoln in the UNSRC identified by M.H. Muma as *S. nesides* are in fact a species of *Walckenaeria* (possibly *W. maesta* Millidge 1983) and an unidentified heterospecific female.

Material examined.—**CANADA:** *Alberta:* Cameron Lake, Waterton Lakes Nat'l Park, 5300 feet, interception trap, 9–28 June 1980, 1♂ (J.M. Campbell, CNC). *British Columbia:* Albert Bay, 50°34'N, 126°58'W, 21 June 1936, 1♀ (Crosby & Bishop, AMNH); Lake Cowichan, moss on log, 8 July 1976, 1♂2♀ (I.M. Smith, CNC); Graham Island, Masset, 1944, 1♂ (M.C. Clark, MCZ); Johnson Bay, Babine Lake, leaf litter, 4 July 1987, 2♂10♀ (R. West, CNC); Malahat, Goldstream Prov. Park, V.I., moss on rock at spring run, 11 July 1979, 3♂13♀ (I. Smith, CNC); Manning Prov. Park, Pitfall in rhododendron flat, 20 June–3 July 1979, 1♀ (Dondale, CNC); Metlakatla, 1♂2♀ (Emerton, AMNH); Prince Rupert, 54°09'N, 130°20'W, 22 June 1936, 1♀ (C.R. Crosby, AMNH); Queen Charlotte Is., Louise Is., Skedans, wet moss at seepage spots on old rd, 8 August 1983, 1♂ (J.M. Campbell, CNC); 7.0 km NW Q.C. City, 4–15 August 1983, flight intercept trap, 2♂ (J.M. Campbell, CNC); Wap Lake, Revelstoke, pitfall -rocky bank, July 1985, 1♀ (M.E. Martin, CNC); Wellington, V.I., 5 October 1949, 4♂10♀ (R. Guppy, AMNH). *Yukon:* Kathleen Lake, Kulane Nat'l Park, litter and stones, 12–15 June 1981, 2♀ (C.D. Dondale, CNC). **UNITED STATES:** *Alaska:* Aleutian Isl., Adak Isl., Andreanof Isl., 26–29 July 1958, 1♀ (C.H. Lindroth, MCZ); Umnak, Fox Islands, July 1958, 1♀ (C. Lindroth, MCZ); Unalaska, Fox Islands, Mt. Makushin, 11–14 July 1958, 1♂4♀ (C. Lindroth, MCZ); Trail to Denver Glacier, Skagway, 25 June 1936, 1♂8♀ (Crosby, AMNH); Haines, Quad. 59°N, 135°W, 20–25 August 1945, 1♀ (Chamberlin, AMNH); Juneau, litter and stones, 8–10 June 1981, 2♀ (C.D. Dondale, CNC), 58°N, 134°W, 28–29 April 1945, 1♀ (Chamberlin,

Table 2.—Quantitative character values for adult males of *Sisicottus* species. Range, mean, standard deviation, and sample size are given for all measurements (in mm). For number of macrosetae in tibial cluster, mode is given in parenthesis.

	<i>S. montigenus</i>	<i>S. quoylei</i>	<i>S. panopeus</i>
Carapace (length)	0.70–0.80 0.74 ± 0.03 n = 20	0.75–0.82 0.78 ± 0.03 n = 6	0.67–0.96 0.87 ± 0.06 n = 20
Metatarsus I (length)	0.40–0.49 0.44 ± 0.03 n = 19	0.39–0.47 0.43 ± 0.03 n = 6	0.50–0.58 0.54 ± 0.02 n = 19
TmI	0.47–0.62 0.56 ± 0.04 n = 19	0.41–0.60 0.54 ± 0.07 n = 6	0.45–0.54 0.50–0.02 n = 19
Palpal tibial apophysis (length)	0.014–0.034 0.023 ± 0.007 n = 22	0.019–0.038 0.031 ± 0.008 n = 6	0.081–0.124 0.102 ± 0.013 n = 20
Palpal tibia (length)	0.138–0.176 0.157 ± 0.011 n = 22	0.147–0.171 0.163 ± 0.008 n = 6	0.238–0.295 0.265 ± 0.016 n = 20
Palpal tibia (width)	0.128–0.166 0.150 ± 0.009 n = 22	0.138–0.162 0.151 ± 0.008 n = 6	0.181–0.223 0.202 ± 0.014 n = 20
Paracymbium (length)	0.095–0.162 0.116 ± 0.016 n = 20	0.109–0.119 0.115 ± 0.004 n = 6	0.133–0.170 0.150 ± 0.008 n = 20
Paracymbium (width)	0.109–0.133 0.120 ± 0.006 n = 20	0.119–0.133 0.124 ± 0.006 n = 6	0.138–0.162 0.152 ± 0.007 n = 20
Lamella characteristica (length)	0.090–0.124 0.107 ± 0.010 n = 20	0.109–0.119 0.112 ± 0.004 n = 6	0.124–0.156 0.138 ± 0.008 n = 20
Number of macrosetae in tibial cluster	3–7 (6) 5.35 ± 1.14 n = 20	3–6 (5) 4.67 ± 1.03 n = 6	7–11 (8) 8.55 ± 0.94 n = 20

AMNH); Primrose Camp, 18 mi. N. of Seward, 60°20'N, 149°20'W, 24 August 1968, 13♂22♀ (W. Ivie, AMNH); 5 mi. S rapids on Richardson Hiway, 26 June 1945, 1♂ (J.C. Chamberlin, AMNH); Skagway, 59°28'N, 135°15'W, 24 June 1939, 2♀ (Crosby, AMNH). *Oregon*: Benton County, Mary's Peak, sod in alder clearing, 28 November 1976, 1♀ (L. Russell, CNC); Latourell Falls, 45°N, 122°W, 4 August 1929, 1♂4♀ (Chamberlin, AMNH); Proxy Falls, Hwy 242, 28 mi. SW Sisters, 3000 feet, *ex* wet moss and debris, depression by waterfall, 19 August 1985, 1♀ (E.E. Lindquist, CNC); Tillamook County, moss near stream, 19 December 1976, 2♀ (L. Russell, CNC). *Washington*: Chelan County, Nason Creek, 47.783°N, 120.874°W, 2280 feet, under rocks by stream, 6 June 1992, 1♂ (Rick Sugg, UWBM); Clallam County, Pillar Pt (W side), 48.220°N, 124.125–130°W, 0–100 feet, *ex* moss on forest floor, 22 May 1987, 2♂ (R. Crawford, UWBM); Emmons Trail, Tainier Park, 46°54'N, 121°39'W, 6 July 1938, 2♀ (Ivie, AMNH); Friday

Harbor, 1924, 1♀ (AMNH); Thurston County, The Evergreen State College, wetland south of Evergreen Parkway, 47°4'10'N, 122°57'39'W, elev. 50 m, *ex* moss on downed *Salix* tree, 16 July 1993, 1♀ (J. Miller, author's personal collection), Woodland SE of Corner of Overhulse Place and Driftwood Road, 47.026°N, 122.962°W, elev. 50 m, 26 October 1992, 1♀ (J. Miller, author's personal collection); Jefferson County, Olympic National Park, Hoh Riv., 510 feet, 47.846°N, 123.960°W, *ex* moss in *Acer macrophyllum*, 29 January 1983, 1♀ (J. Longino, UWBM); Lewis County, Lewis & Clark S.P., 46.519°N, 122.815°W, 380 feet, *ex* leaf litter, 29 October 1988, 1♂1♀ (R. Crawford, UWBM); King County, E. of Change Creek, 1250 feet, 47°44'N, 121°66'W, wet moss and litter in and near seepage, 7 July 1996, 3♂4♀ (J. & C. Zujko-Miller, J. & H. Miller, author's personal collection); King County, W of Change Cr., 1280 feet, 47.439°N, 121.633°W, 9 April 1989, 2♂6♀ (R. Crawford, UWBM); King County, Happy Valley bog, 47.640°N, 122.017°W,

Table 2.—Extended.

<i>S. montanus</i>	<i>S. crossoclavis</i>	<i>S. cynthiae</i>	<i>S. orites</i>	<i>S. nesides</i>
0.71–0.93	0.83–0.97	1.00–1.10	0.93–1.20	0.99–1.24
0.86 ± 0.04	0.88 ± 0.08	1.04 ± 0.04	1.07 ± 0.07	1.10 ± 0.08
<i>n</i> = 56	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 22
0.45–0.58	0.51–0.66	0.67–0.74	0.66–0.81	0.71–0.83
0.52 ± 0.03	0.58 ± 0.07	0.71 ± 0.02	0.73 ± 0.05	0.77 ± 0.03
<i>n</i> = 53	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 19
0.45–0.65	0.49–0.56	0.49–0.58	0.42–0.56	0.47–0.60
0.58 ± 0.04	0.52 ± 0.04	0.54 ± 0.03	0.50 ± 0.03	0.54 ± 0.04
<i>n</i> = 53	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 19
0.043–0.076	0.124–0.171	0.067–0.090	0.105–0.162	0.081–0.114
0.058 ± 0.007	0.155 ± 0.027	0.079 ± 0.009	0.126 ± 0.014	0.096 ± 0.011
<i>n</i> = 57	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 39	<i>n</i> = 21
0.162–0.228	0.261–0.333	0.257–0.318	0.266–0.337	0.242–0.323
0.193 ± 0.012	0.306 ± 0.039	0.295 ± 0.023	0.306 ± 0.020	0.289 ± 0.021
<i>n</i> = 57	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 22
0.152–0.185	0.209–0.228	0.176–0.219	0.185–0.261	0.162–0.233
0.172 ± 0.009	0.217 ± 0.010	0.200 ± 0.015	0.229 ± 0.019	0.120 ± 0.016
<i>n</i> = 57	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 22
0.105–0.152	0.143–0.166	0.124–0.171	0.152–0.195	0.157–0.195
0.130 ± 0.009	0.157 ± 0.013	0.155 ± 0.015	0.175 ± 0.011	0.174 ± 0.010
<i>n</i> = 57	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 22
0.119–0.152	0.143–0.147	0.152–0.176	0.133–0.190	0.143–0.181
0.136 ± 0.006	0.146 ± 0.003	0.165 ± 0.009	0.178 ± 0.011	0.166 ± 0.008
<i>n</i> = 57	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 22
0.100–0.133	0.128–0.162	0.133–0.143	0.143–0.176	0.124–0.157
0.121 ± 0.007	0.143 ± 0.017	0.138 ± 0.004	0.159 ± 0.009	0.145 ± 0.009
<i>n</i> = 57	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 22
2–6 (4)	7–9 (9)	6–8 (7)	8–13 (9)	7–10 (7)
4.16 ± 0.80	8.33 ± 1.16	7.22 ± 0.67	9.38 ± 1.11	7.68 ± 0.72
<i>n</i> = 57	<i>n</i> = 3	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 22

125 feet, sifted in deciduous litter, 11 October 1980, 1♂ (R. Crawford, UWBM); Snohomish County, Lake Twentytwo Research Natural Area, trail head, old growth forest, sifted from moss on log, 25 June 1993, 4♀ (J. Miller, author's personal collection); Mt. Rainier Nat. Park, Nisqually River, 3900 feet, 8 August 1973, 1♂11♀ (A. Smetana, CNC); Mt. Rainier Nat. Park, North Puyallup River, 3700 feet, 10 August 1973, 7♀ (A. Smetana, CNC); Paradise, Rainier Nat'l Park, 46°48'N, 121°44'W, 12 September 1965, 3♂10♀ (J. & W. Ivie, AMNH); Pend Oreille County, Deemer Creek, 48.931°N 117.089°W, 4600 feet, sifted from soggy moss at stream edge, 13 June 1986, 1♂ (R. Crawford, UWBM); 4 mi. N Silver Fir Cmpg., Mt Baker, 4000 feet, 16 August 1975, 1♀ (J.M. Campbell, CNC); Skagit County, E of Swede Cr., 48.562–65°N, 122.216°W, 350 feet, *ex* mixed leaf litter, 19 March 1988, 1♀ (R. Crawford, UWBM); 10 miles north of Vancouver, 45°45'N, 122°38'W, 10 September 1935, 1♀ (Chamberlin & Ivie, AMNH); Whatcom

County, Blue Lake Trail, 48.652°N, 121.786°W, 5000 feet, *ex* rotten log, 13 September 1986, 1♀ (R. Crawford, UWBM); Yakima County, Bear Creek Mtn Trail, 46.552°N, 121.315°W, 6160 feet, ♂ *-ex* wet moss by stream, ♀ *-ex* rotten log, 4 September 1986, 1♂1♀ (R. Crawford, UWBM).

Sisicottus aenigmaticus new species
Figs. 72, 100, 106–108

Sisicottus orites: Crawford 1988: 15 (misidentification). Crawford & Edwards 1988: 437; figs. 25–26 [♀] (misidentification).

Types.—Female holotype from UNITED STATES: Washington, King County, W. of Change Cr. 1280 feet, 47.439°N, 121.663°W, *ex* moss in & nr spring, 22 August 1981, R.E. Nelson, deposited in UWBM.

Etymology.—The specific name is a Latin adjective meaning enigmatic.

Table 3.—Quantitative character values for adult females of *Sisicottus* species. *Sisicottus aenigmaticus* is the female holotype alone. For all other species, range, mean, standard deviation, and sample size are given (in mm). Ventral plate invagination width is poorly defined in *S. panopeus*, *S. montanus*, and *S. crossoclavis* and was not recorded for these species.

	<i>S. montigenus</i>	<i>S. quoylei</i>	<i>S. panopeus</i>	<i>S. montanus</i>
Carapace (length)	0.67–0.80 0.74 ± 0.03 n = 33	0.71–0.80 0.76 ± 0.02 n = 12	0.82–0.95 0.88 ± 0.04 n = 21	0.72–0.88 0.81 ± 0.04 n = 57
Metatarsus I (length)	0.31–0.46 0.42 ± 0.03 n = 33	0.35–0.42 0.39 ± 0.02 n = 10	0.45–0.56 0.50 ± 0.03 n = 21	0.39–0.52 0.45 ± 0.03 n = 57
TmI	0.48–0.77 0.60 ± 0.05 n = 33	0.52–0.63 0.58 ± 0.04 n = 10	0.45–0.73 0.52 ± 0.06 n = 21	0.50–0.75 0.59 ± 0.04 n = 57
Epigynum (length)	0.124–0.176 0.149 ± 0.012 n = 33	0.109–0.128 0.130 ± 0.010 n = 12	0.114–0.162 0.139 ± 0.012 n = 22	0.095–0.166 0.148 ± 0.012 n = 59
Copulatory duct capsule (width)	0.124–0.176 0.149 ± 0.012 n = 33	0.114–0.152 0.130 ± 0.010 n = 12	0.105–0.162 0.133 ± 0.014 n = 22	0.109–0.176 0.138 ± 0.015 n = 59
Dorsal plate posterior face (width)	0.081–0.119 0.099 ± 0.010 n = 33	0.076–0.105 0.089 ± 0.008 n = 12	0.076–0.100 0.085 ± 0.008 n = 22	0.067–0.114 0.087 ± 0.011 n = 59
Dorsal plate posterior face (height)	0.105–0.138 0.118 ± 0.009 n = 33	0.081–0.124 0.112 ± 0.011 n = 12	0.081–0.109 0.096 ± 0.009 n = 22	0.071–0.114 0.088 ± 0.008 n = 59
Ventral plate invagination (depth)	0.090–0.119 0.095 ± 0.008 n = 29	0.071–0.081 0.075 ± 0.004 n = 12	0–0.024 0.010 ± 0.005 n = 22	0.005–0.033 0.019 ± 0.006 n = 59
Ventral plate invagination (width)	0.062–0.109 0.080 ± 0.012 n = 33	0.014–0.043 0.032 ± 0.009 n = 12		

Diagnosis.—Males are unknown, but are probably similar to *S. orites* and *S. nesides*. Females of *S. aenigmaticus*, *S. orites*, and *S. nesides* differ from those of all other *Sisicottus* species by the form of the copulatory duct capsule in dorsal view which has strongly bowed lateral margins (Fig. 108, character 31); in all other species, the lateral margins are sinuous to moderately bowed. They are distinguished from all other *Sisicottus* species except *S. montigenus* by their very wide ventral plate invagination (Fig. 106). The dorsal plate with a trapezoidal posterior face is unique in *Sisicottus* (Fig. 107, character 21). They also differ from all other *Sisicottus* species in having smaller, more widely spaced spermathecae with very narrow margins and copulatory ducts with a relatively narrow proximal part (Fig. 108).

Description.—Large (carapace length = 0.91 mm); single known specimen lighter than nor-

mal (see remarks below). Ventral plate invagination deep and wide (Fig. 106). Posterior face of dorsal plate trapezoidal, flat ventrally, widest dorsally with concave sides (Fig. 107). Dorsal fold of dorsal plate sclerotized (Fig. 108). Lateral margins of copulatory duct capsule in dorsal view strongly bowed with the tips of the capsule oriented mesally toward each other; spermathecae relatively small with very narrow margins; copulatory ducts relatively narrow and sinuous; anterior margin of capsule formed into two convex lateral lobes; fertilization ducts looped (Fig. 108). See Table 3.

Remarks.—This species is known from a single female specimen. It is lightly sclerotized in a way that is characteristic of specimens that have only recently molted to the adult instar. This specimen may be a mutant individual of *S. nesides*, which has also been collected at the Change Creek site, but I think it more likely that it is a member of a distinct

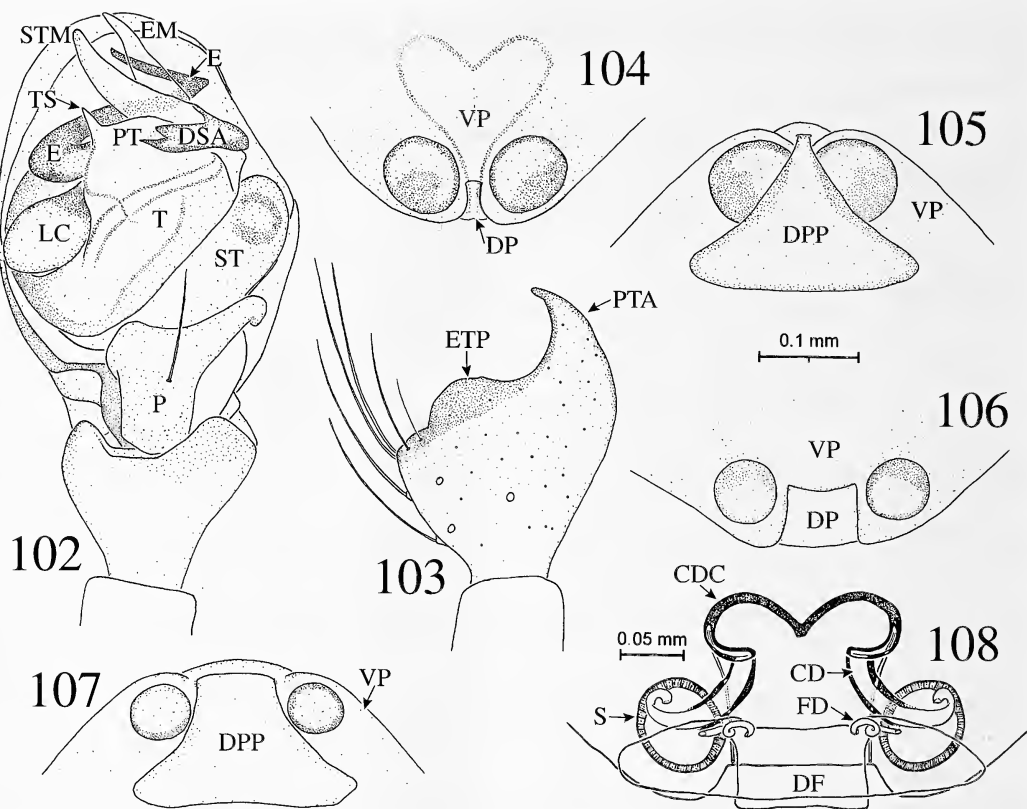
Table 3.—Extended.

<i>S. crossoclavis</i>	<i>S. cynthiae</i>	<i>S. orites</i>	<i>S. nesides</i>	<i>S. aenigmaticus</i>
0.81–0.90	0.88–1.06	0.88–1.13	0.86–1.12	0.91
0.85 ± 0.04	0.98 ± 0.05	1.00 ± 0.06	0.97 ± 0.07	
<i>n</i> = 13	<i>n</i> = 15	<i>n</i> = 72	<i>n</i> = 45	
0.43–0.53	0.60–0.74	0.55–0.78	0.58–0.71	0.63
0.5 ± 0.03	0.67 ± 0.04	0.65 ± 0.05	0.65 ± 0.04	
<i>n</i> = 13	<i>n</i> = 14	<i>n</i> = 71	<i>n</i> = 39	
0.44–0.54	0.45–0.60	0.34–0.62	0.48–0.63	0.55
0.50 ± 0.03	0.56 ± 0.05	0.51 ± 0.04	0.54 ± 0.03	
<i>n</i> = 12	<i>n</i> = 14	<i>n</i> = 71	<i>n</i> = 39	
0.138–0.166	0.128–0.162	0.152–0.209	0.133–0.181	0.14
0.156 ± 0.009	0.144 ± 0.010	0.179 ± 0.013	0.150 ± 0.010	
<i>n</i> = 13	<i>n</i> = 15	<i>n</i> = 73	<i>n</i> = 50	
0.105–0.147	0.128–0.162	0.143–0.238	0.100–0.176	0.12
0.130 ± 0.013	0.144 ± 0.010	0.187 ± 0.023	0.145 ± 0.016	
<i>n</i> = 13	<i>n</i> = 15	<i>n</i> = 73	<i>n</i> = 50	
0.105–0.143	0.109–0.152	0.124–0.204	0.143–0.228	0.21
0.126 ± 0.014	0.135 ± 0.012	0.165 ± 0.018	0.181 ± 0.019	
<i>n</i> = 13	<i>n</i> = 15	<i>n</i> = 73	<i>n</i> = 50	
0.100–0.124	0.086–0.133	0.109–0.181	0.105–0.171	0.152
0.112 ± 0.007	0.108 ± 0.014	0.152 ± 0.016	0.147 ± 0.014	
<i>n</i> = 13	<i>n</i> = 15	<i>n</i> = 73	<i>n</i> = 50	
0–0.019	0.014–0.038	0.052–0.090	0.043–0.086	0.062
0.011 ± 0.005	0.023 ± 0.007	0.074 ± 0.009	0.058 ± 0.009	
<i>n</i> = 13	<i>n</i> = 15	<i>n</i> = 60	<i>n</i> = 49	
	0.014–0.043	0.005–0.043	0.005–0.043	0.067
	0.023 ± 0.007	0.022 ± 0.009	0.020 ± 0.008	
	<i>n</i> = 15	<i>n</i> = 73	<i>n</i> = 49	

species. Since syntopy is common for *Sisicottus* species, I do not regard the fact that *S. nesides* have been collected at the type locality of *S. aenigmaticus* as evidence that the latter is an aberrant form of the former. Of course, the collection of more specimens will be needed in order to test this hypothesis. The Change Creek collection site has yielded a number of other rare and unique spiders including undescribed species of the linyphiid genera *Hal-*

Table 4.—Quantitative character values for male holotype specimens of *Sisicottus* species. Data for the female holotype of *S. aenigmaticus* are given in Table 3. All measurements in mm.

	<i>S. montigenus</i>	<i>S. quoylei</i>	<i>S. panopeus</i>	<i>S. montanus</i>	<i>S. crossoclavis</i>	<i>S. cynthiae</i>	<i>S. orites</i>	<i>S. nesides</i>
Carapace length	0.75	0.75	0.88	0.89	0.97	1.00	0.97	1.00
Metatarsus I length		0.39	0.52	0.48	0.66	0.68	0.68	
TmI		0.41	0.45	0.64	0.56	0.54	0.54	
Palpal tibial apophysis length	0.02	0.04	0.09	0.06	0.17	0.08	0.12	0.09
Palpal tibia length	0.16	0.15	0.23	0.17	0.32	0.3	0.29	0.28
Palpal tibia width	0.15	0.15	0.2	0.19	0.23	0.2	0.19	0.16
Paracymbium length	0.11	0.11	0.16	0.13	0.17	0.17	0.18	0.17
Paracymbium width	0.12	0.12	0.15	0.13	0.15	0.16	0.15	0.14
Lamella length	0.14	0.11	0.14	0.12	0.16	0.14	0.14	0.13
Macrosetae in tibial cluster	3	6	7	4	7	7	10	7



Figures 102–108.—*Sisicottus nesides* and *S. aenigmaticus*. 102–105, *S. nesides* from Primrose Camp, Alaska. 102, Palpus, ventral view; 103, Palpal tibia, dorsal view; 104, Epigynum, ventral view; 105, Epigynum, posterior view. 106–108, Epigynum of *S. aenigmaticus* holotype from Change Creek, Washington. 106, Ventral view; 107, Posterior view; 108, Cleared, dorsal view. Scales: Fig. 108 = 0.05 mm; other figures = 0.1 mm.

orates Hull 1911 and *Eulaira* Chamberlin & Ivie 1933, and something that may belong to the dictynid genus *Saltonia* Chamberlin & Ivie 1942 (R. Crawford pers. comm.).

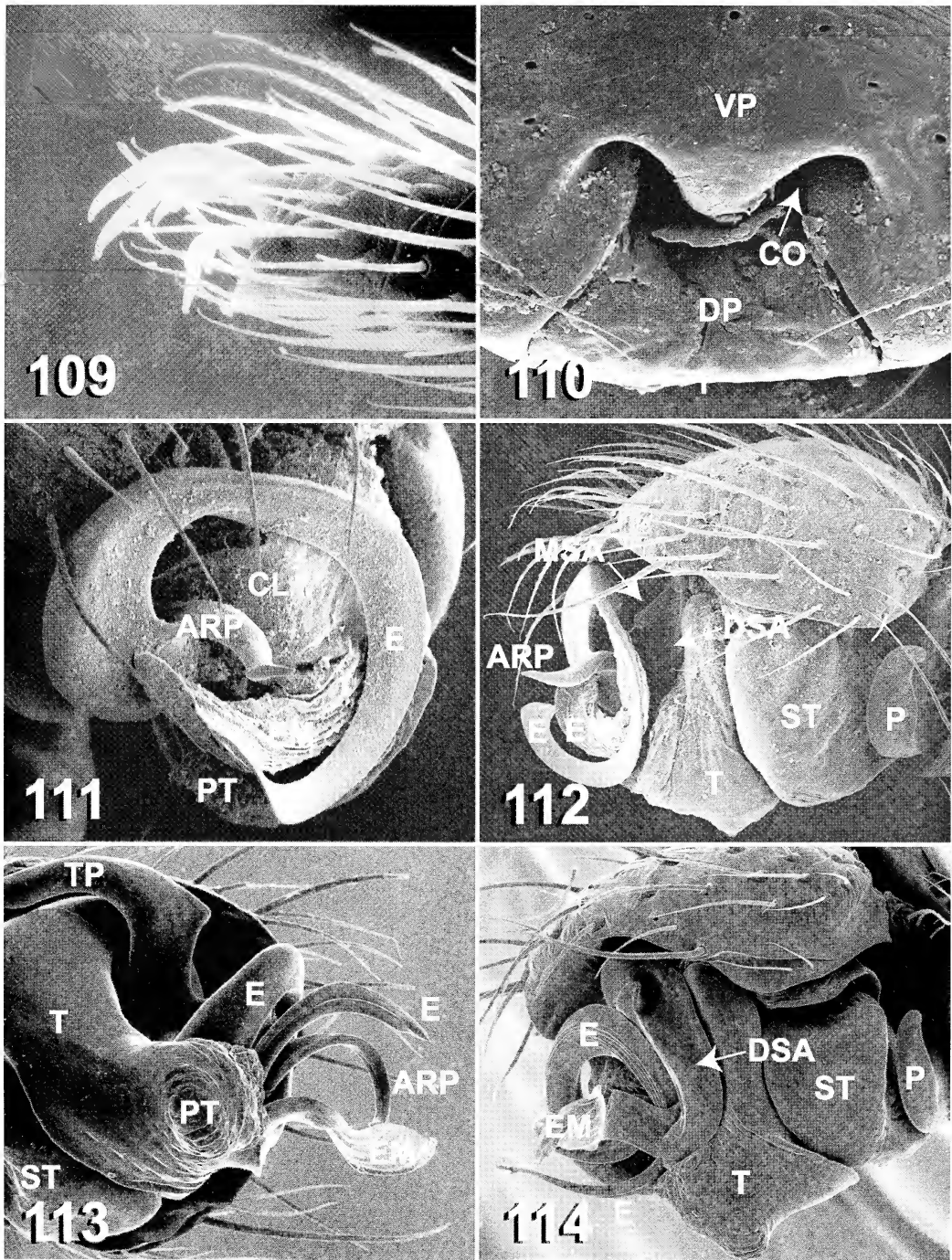
Natural history.—The single specimen was collected from moss in and near a spring.

Distribution.—Known only from the type locality (Fig. 72).

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Figures 109–114.—Scanning electron micrographs of *Sisicottus* and *Typhochrestus*. 109, Tarsal claw of female *Sisicottus panopeus* from Mt. Rainier, Washington. 110–112, *Typhochrestus uintanus* from Mirror Lake, Utah. 110, Epigynum, ventral view; 111, Palpus, apical view; 112, Palpus, ectal view. 113, 114, *Typhochrestus digitatus* from Whiteford Burrows, England. 113, Palpus, ventral view; 114, Palpus, ectal view.

Table 5.—Data matrix, characters and states. Number of steps (St), consistency index (CI), retention index (RI), and rescaled consistency index (RC) are from the preferred most parsimonious tree. “?” = unknown; “—” = not applicable.

Characters and states	<i>Is-</i> <i>landi-</i> <i>ana</i> <i>prin-</i> <i>ceps</i>	<i>Diplo-</i> <i>cent-</i> <i>ria</i> <i>biden-</i> <i>tata</i>	<i>Ty-</i> <i>pho-</i> <i>chres-</i> <i>digit-</i> <i>atus</i>	<i>Ty-</i> <i>pho-</i> <i>chres-</i> <i>uin-</i> <i>tanus</i>	<i>Eri-</i> <i>gone</i> <i>psych-</i> <i>ro-</i> <i>phila</i>	<i>Tme-</i> <i>ticus</i> <i>tolli</i>	<i>Wal-</i> <i>cken-</i> <i>aeria</i> <i>di-</i> <i>recta</i>	<i>Gona-</i> <i>tium</i> <i>ru-</i> <i>bens</i>
Male palpus								
1. embolus: short; long	0	0	1	1	0	0	1	1
2. terminal embolic hook: abs; pres	0	0	0	0	0	0	0	0
3. DSA sclerotization: mem; light; heavy	1	1	0	1	2	1	1	1
4. DSA: short; long	0	0	0	0	1	0	0	0
5. STM: absent; present	0	0	0	0	0	0	0	1
6. MSA: absent; present	0	1	1	1	0	0	0	0
7. TP: present; absent	0	0	0	0	0	0	0	0
8. TP shape: straight; spiral; ectal; anterior	2	0	1	1	3	0	1	0
9. LC: absent; present	0	0	0	0	0	0	0	1
10. ARP: absent; present	1	1	1	1	1	1	0	0
11. ARP shape: short; long and spiral	0	0	1	1	0	0	—	—
12. PT papillae: absent; present	1	1	1	1	0	0	0	—
13. TS: absent; present	0	0	0	0	0	1	0	1
14. P, ventral view: narrow; wide	0	0	0	0	0	0	0	0
15. CE: small; large	1	0	0	0	1	0	0	1
16. TA length: short; long	0	1	0	0	1	1	0	0
17. ETP: strong; weak or absent	1	0	0	1	0	0	0	0
18. patella apophysis: absent; present	0	0	0	0	1	1	0	0
Female genitalia								
19. VP: beyond EF; shallow inv; deep inv	0	0	2	2	0	2	2	2
20. median VP: convex; concave	0	0	0	0	1	0	1	1
21. DPP: rect; invert tri; tri; trapezoid	1	0	0	0	1	0	0	2
22. sides DPP: convex; concave	0	0	0	0	0	0	0	0
23. vent mar DPP: concave; convex	1	0	0	0	1	1	1	1
24. DF sclerotization: light; heavy	0	0	0	0	0	0	0	0
25. CO: small; large	1	0	0	1	0	0	1	1
26. CD origin: ectal; mesal	1	0	1	1	1	1	1	1
27. CD anterior proj: absent; present	0	0	1	1	1	0	0	1
28. CD encapsulation: absent; present	0	0	1	0	1	1	1	0
29. CDC: partial; complete	—	—	1	—	1	0	1	—
30. ant lat CDC: concave; straight; convex	—	—	0	—	0	—	1	—
31. lat mar CDC: curved; bowed	—	—	0	—	0	—	0	—
32. post CDC orientation: post; mesal	—	—	0	—	0	0	0	—
33. FD origin: posterior; mesal	1	0	1	1	1	1	1	1
34. FD shape: sinuous; spiral	0	1	0	0	0	0	0	1
Somatic morphology								
35. cephalic region: not raised; raised	0	0	0	0	1	0	0	1
36. post PME lobe: absent; present	0	0	1	0	0	0	0	0
37. cuticular pores: absent; present	0	0	1	?	0	0	1	0
38. cheliceral file: ridged; scaly; imb	2	2	2	?	2	1	0	1
39. dorsal spur: absent; present	0	0	0	0	0	1	0	0
40. tibia III m-setae: two; one	0	1	0	0	0	1	1	1
41. Tm IV: absent; present	0	0	0	0	1	1	1	1

Table 5.—Extended.

<i>Gon- gyl- dium</i>	<i>Oedo- tho- rax</i>	<i>Sisi- cottus</i>	<i>Sisi- cottus</i>	<i>Sis- cottus</i>	<i>Sis- cottus</i>	<i>Sis- cottus</i>	<i>Sis- cottus</i>	<i>Sisi- cottus</i>	<i>Sisi- cottus</i>	<i>Sisi- cottus</i>	<i>Sisi- cottus</i>	St	CI	RI	RC
<i>ruf- ipes</i>	<i>gibo- sus</i>	<i>monti- genus</i>	<i>quoy- lei</i>	<i>pano- peus</i>	<i>mont- anus</i>	<i>cross- ocla- vis</i>	<i>cottus</i>	<i>cyn- thiae</i>	<i>cottus</i>	<i>nesi- des</i>	<i>aenig- maticus</i>				
1	1	1	1	1	1	1	1	1	1	1	?	2	0.50	0.67	0.33
0	0	1	1	1	1	1	1	1	1	1	?	1	1.00	1.00	1.00
1	1	0	1	1	1	2	2	2	2	2	?	4	0.50	0.60	0.30
1	0	1	1	0	0	0	1	1	1	1	?	4	0.25	0.50	0.13
0	0	1	1	1	1	1	1	1	1	1	?	2	0.50	0.88	0.44
0	1	1	1	1	1	1	1	1	1	1	?	2	0.50	0.80	0.40
1	1	1	1	1	1	1	1	1	1	1	?	1	1.00	1.00	1.00
—	—	—	—	—	—	—	—	—	—	—	?	4	0.75	0.50	0.38
1	1	1	1	1	1	1	1	1	1	1	?	1	1.00	1.00	1.00
0	0	0	0	0	0	0	0	0	0	0	?	1	1.00	1.00	1.00
—	—	—	—	—	—	—	—	—	—	—	?	1	1.00	1.00	1.00
1	1	1	1	1	1	1	1	1	1	1	?	2	0.50	0.50	0.25
1	1	1	1	1	1	1	1	1	1	1	?	2	0.50	0.80	0.40
1	0	1	1	1	1	1	1	1	1	1	?	2	0.50	0.88	0.44
1	1	1	1	1	1	1	1	1	1	1	?	3	0.33	0.50	0.17
0	0	1	1	0	0	0	0	0	0	0	?	4	0.25	0.25	0.06
0	0	1	1	1	0	1	0	0	0	0	?	5	0.20	0.20	0.04
0	0	0	0	0	0	0	0	0	0	0	?	2	0.50	0	0
2	2	2	2	1	1	1	1	2	2	2	2	4	0.50	0.60	0.30
0	1	1	1	1	1	1	1	1	1	1	1	3	0.33	0.60	0.20
2	0	0	0	0	1	1	1	1	1	1	3	6	0.50	0.57	0.29
0	0	0	0	0	0	0	0	0	0	1	1	1	1.00	1.00	1.00
1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	1.00	1.00
0	0	0	0	0	0	1	1	1	1	1	1	1	1.00	1.00	1.00
1	0	0	0	0	0	0	0	0	0	0	0	4	0.25	0.25	0.06
1	1	0	0	0	0	0	0	0	0	0	0	2	0.50	0.88	0.44
0	1	1	1	1	1	1	1	1	1	1	1	4	0.25	0.25	0.06
1	1	1	1	1	1	1	1	1	1	1	1	3	0.33	0.33	0.11
1	0	1	1	1	1	1	1	1	1	1	1	2	0.50	0	0
1	—	1	1	2	2	2	2	2	2	2	2	2	1.00	1.00	1.00
0	—	0	0	0	0	0	0	1	1	1	1	1	1.00	1.00	1.00
0	0	0	0	0	0	0	1	1	1	1	1	1	1.00	1.00	1.00
1	0	1	1	1	1	1	1	1	1	1	1	2	0.50	0	0
0	0	0	0	0	0	1	1	1	1	1	1	3	0.33	0.67	0.22
0	0	0	0	0	0	0	0	0	0	0	?	2	0.50	0	0
0	1	0	0	0	0	0	0	0	0	0	?	2	0.50	0	0
0	1	0	0	0	0	0	0	0	0	0	?	3	0.33	0	0
1	1	2	2	2	2	2	2	2	2	2	2	3	0.67	0.67	0.44
1	1	0	0	0	0	0	0	0	0	0	?	3	0.33	0	0
1	1	0	0	0	0	0	0	0	0	0	0	3	0.33	0.60	0.20
1	1	0	0	0	0	0	0	0	0	0	0	2	0.50	0.80	0.40

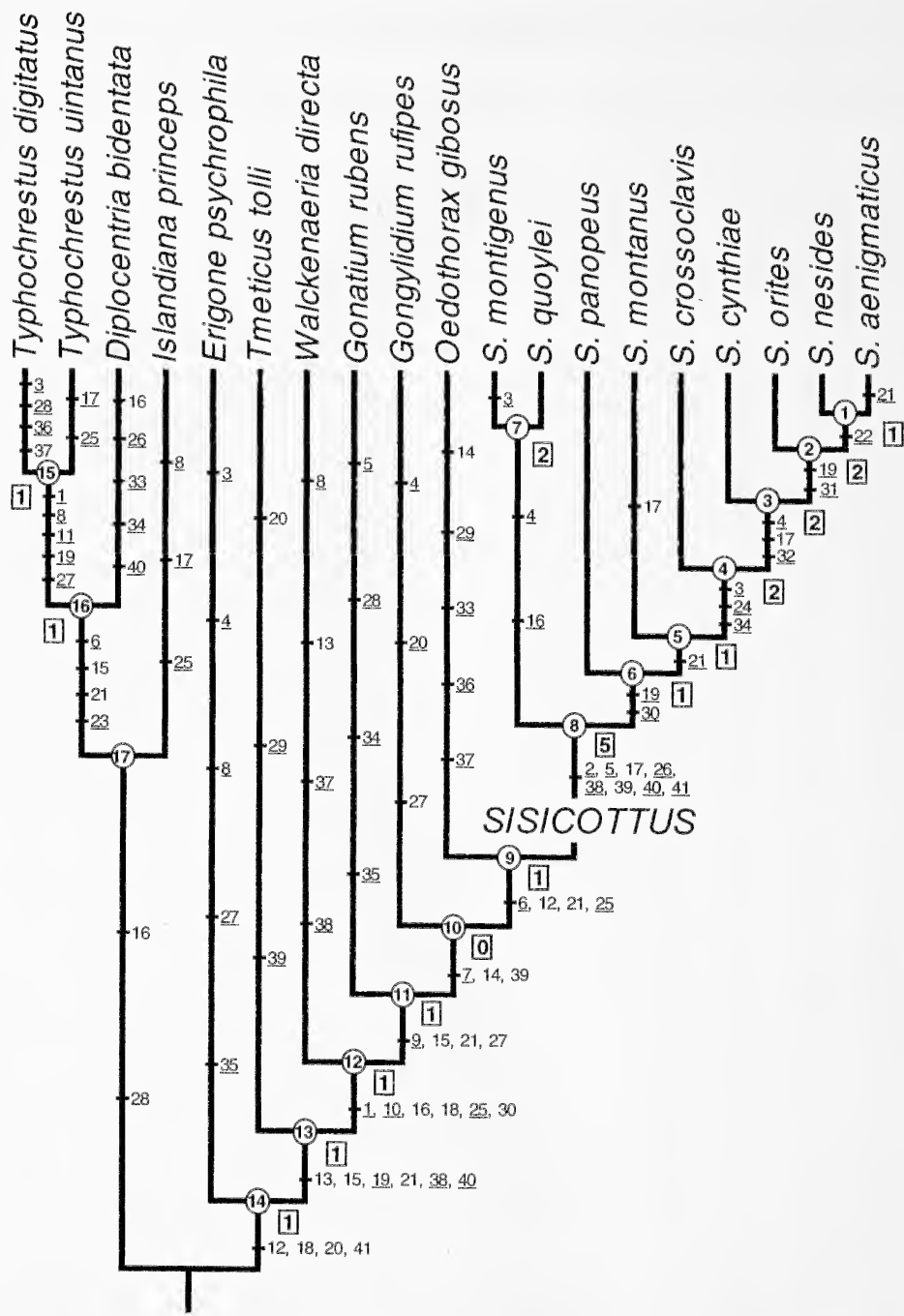


Figure 115.—Preferred most parsimonious cladogram of *Sisicottus* species based on successive character weighting and implied weights. Underlined numbers indicate unambiguous character change optimizations; the remaining characters were optimized to favor reversal over parallel evolution (Farris optimization) unless explicitly justified in the text. Bremer support values appear as boxed numbers to the right of each applicable internode. The circled numbers at each node identify clades discussed in the text.

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Note added in proof: Dondale (1990) included two illustrations labeled “*Sisicottus* sp.” in his key to litter-inhabiting spiders in North America. Although there is no documentation of what specimens the illustrations were based on, his figure 17.142 is probably the palpal tibia of *S. quoylei*; his figure 17.157 is probably the epigynum of *S. montanus*.

RADIATION OF THE GENUS *DYSDERA* (ARANEAE, DYSDERIDAE) IN THE CANARY ISLANDS: THE ISLAND OF TENERIFE

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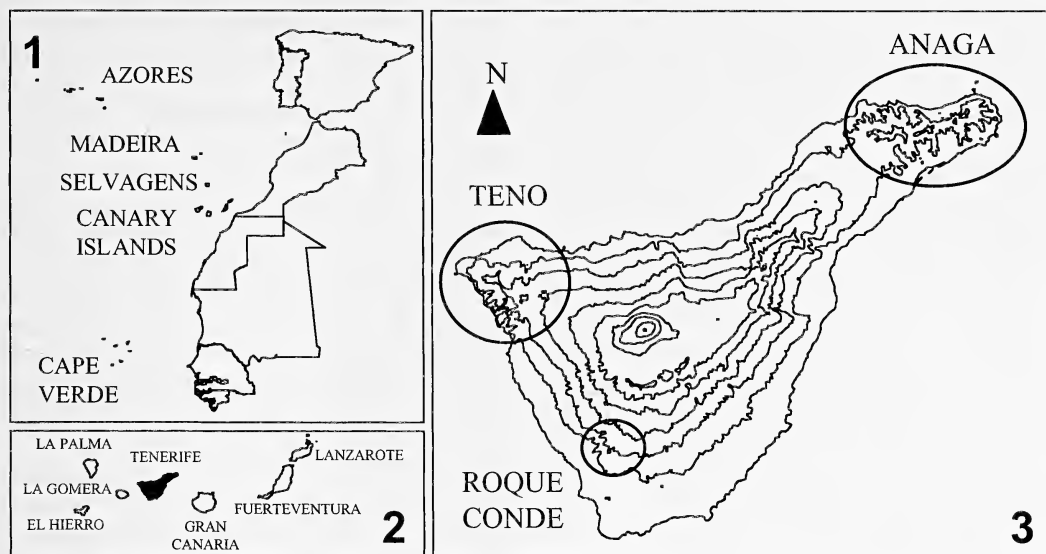
ABSTRACT. An overwhelming number of endemic species belonging to the spider genus *Dysdera* have been reported from the oceanic archipelago of the Canary Islands. A complete taxonomic revision is currently being performed in order to assess the extent of this species' radiation, as well as to supply enough data to place it in a phylogenetic framework. The present article is devoted to the *Dysdera* species inhabiting the island of Tenerife. A total of 22 species is recognized in Tenerife, including the cosmopolitan *Dysdera crocata* C.L. Koch 1839. Two new species are described: *Dysdera guayota* new species and *Dysdera hernandezi* new species. Ten new synonymies are reported: *D. moquinalensis* Wunderlich 1991 and *D. vilaflorensis* Wunderlich 1991 = *D. brevispina* Wunderlich 1991; *D. medinae* Wunderlich 1991 = *D. cribellata* Simon 1883; *D. inaequuscapillata* Wunderlich 1991 = *D. crocata*; *D. pergrada* Wunderlich 1991, *D. pseudopergrada* Wunderlich 1991, *D. tabaibaensis* Wunderlich 1991, *D. teideensis* Wunderlich 1991 and *D. teneriffensis* Strand 1908 = *D. macra* Simon 1883; *D. obscuripes* Wunderlich 1991 = *D. propinqua* Ribera, Ferrández & Blasco 1985. Sixteen species are redescribed: *D. ambulotenta* Ribera, Ferrández & Blasco 1985; *D. brevisetae* Wunderlich 1991, *D. brevispina* Wunderlich 1991; *D. chioensis* Wunderlich 1991; *D. cribellata* Simon 1883; *D. curvisetae* Wunderlich 1987; *D. esquiveli* Ribera & Blasco 1986; *D. gibbifera* Wunderlich 1991; *D. gollumi* Ribera & Arnedo 1994; *D. labradaensis* Wunderlich 1991; *D. macra* Simon 1883; *D. minutissima* Wunderlich 1991; *D. montanetensis* Wunderlich 1991; *D. propinqua* Ribera, Ferrández & Blasco 1985; *D. unguimmanis* Ribera, Ferrández & Blasco 1985 and *D. volcania* Ribera, Ferrández & Blasco 1985. The females of four species: *D. brevisetae*, *D. brevispina*, *D. minutissima* and *D. montanetensis* are described for the first time. Females formerly assigned to both *D. gibbifera* and *D. volcania* are considered to be incorrect identifications. A neotype is designated for *D. macra*. The presence of *D. rugichelis* Simon 1907 in Tenerife is considered to be doubtful. Ecological and distributional patterns of the species are discussed.

Species of the spider genus *Dysdera* Latreille 1804 are usually found in slightly damp but warm ground habitats. They are nocturnal wandering hunters that spend daytime in silken cocoons under stones, logs or bark (Roberts 1995; pers. obs.). *Dysdera* specimens are not unusual in caves, which can be considered as an expansion of their typical habitats; and several cases of troglomorphic species have been reported (Ribera 1983, 1993; Ribera et al. 1986). This species-rich genus includes about 200 species with a circum-Mediterranean distribution, with the single exception of the anthropophilous cosmopolitan *D. crocata* C.L. Koch 1839. The so-called Macaronesian archipelagos (Fig. 1) represent the westernmost limit of *Dysdera*'s range. One of these

volcanic archipelagos, the Canary Islands, harbors about 50 endemic species (Simon 1883, 1907; Strand 1908; Schmidt 1973; Ribera et al. 1985; Ribera & Blasco 1986; Wunderlich 1987, 1991; Ribera & Arnedo 1994; Arnedo et al. 1996; Arnedo & Ribera 1997), which represent about one quarter of the described species in the genus to date. This figure is even more remarkable when compared with the number of endemics in the remaining archipelagos: one from the Azores (undescribed species), five from Madeira (Denis 1962; Wunderlich 1994) and one from Cape Verde (Berland 1936). In addition, seven of these species were troglobites with morphological adaptations to the hypogean environment.

Nevertheless, this overwhelming number of *Dysdera* species held by the Canaries could suggest a taxonomic artifact instead of a true species radiation. A deeper look into Canarian *Dysdera* taxonomy revealed some instances

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Figures 1–3.—Maps 1–3. 1, Macaronesian archipelagos; 2, the Canary Islands; 3, Tenerife, with its oldest areas encircled.

that could, at least, call into question this amazing number of endemics. On the one hand, 22 out of the 50 recognized species were described from only one of the sexes, 19 of which were known from a single specimen. Moreover, some of the species lacked information regarding their locality, type material was lost, or both. Finally, 27 species were described in a single publication together with 106 new species from the Macaronesia (Wunderlich 1991). On the other hand, most of the published descriptions of the Canarian *Dysdera* were vague enough to correspond to more than one species, or failed to supply the necessary information for the study of such interesting spiders in a phylogenetic framework.

With the aim of confirming the existence of this radiation, completing the species descriptions as well as their geographical distributions and, finally, offering enough data to perform a phylogenetic analysis of the group, a major revisionary work on Canarian *Dysdera* is currently being developed (Ribera & Arnedo 1994; Arnedo & Ribera 1996; Arnedo et al. 1996; Arnedo & Ribera 1997). The present article is devoted to the taxonomic revision of the genus on the Island of Tenerife.

The Canary Islands lie in the Atlantic Ocean 100 km from the north-western coast of Africa (Fig. 2). The different volcanic ep-

isodes that formed the archipelago are probably the result of a propagating fracture originated in the Atlas formation during the Alpine orogeny, about 25 Mya ago (Anguita & Hernán 1975). This model would explain both the reduction of the age of the islands from east to west and the continuation of active volcanism in the older islands. The approximate ages of the subaerial parts of the islands, as recovered using the K-Ar technique, range from about 22 Mya to less than 1 Mya. The estimated geological age for each island is: Fuerteventura 20–22 Mya, Lanzarote 15–19 Mya, Gran Canaria 14–16 Mya, Tenerife 11.6–14 Mya, La Gomera 10–12 Mya, La Palma 1.6–2 Mya and El Hierro 0.8–1 Mya (Cantagrel et al. 1984, Mitchell-Thomé 1985, Ancochea et al. 1990, Coello et al. 1992). The island of Tenerife is located roughly at the center of the line drawn through the archipelago. Tenerife is both the biggest (2058 km²) and the highest (3717 m) island in the archipelago.

Elevation together with trade winds play important ecological roles on oceanic islands, especially at tropical and subtropical latitudes. They are both responsible for the presence and distribution of the different ecological zones. In the particular case of the Canaries, the joint effect of the humid and cool NE trade winds, between altitudes of 400–1200 m, and the dry

trade winds from the NW, above 2000 m, cause a temperature inversion. In this area, a nearly permanent cloud belt is formed. Consequently, strong ecological segregation is observed between northern, more humid, and southern, dryer slopes. Five major ecological zones can be recognized on northern slopes of the islands. The first, from the seashore to up to 250 m, is characterized by the presence of dry-arid subtropical shrubs. The second, from 250–600 m, features humid to semi-arid tropical shrubs and woods. The third, from 600–1000 m, is covered by the cloud belt and features a typical subtropical wood, the so-called laurel forest. In the fourth, from 1000–2000 m, an endemic pine forest occurs. Finally, dry subalpine shrub is present from 2000 m to the top. Southern slopes lack a laurel forest zone and transition between sub-arid shrubs and the pine forest takes place at higher elevation.

Apart from these climatic-related ecosystems, an additional ecological zone is present in volcanic islands: the hypogean environment. The subterranean environment in the Canaries is represented by both lava tubes and the MSS (mesocavernous shallow stratum) (Juberthie et al. 1980, 1981; Oromí et al. 1986; Medina 1991). Due to their short lifespan, lava tubes are found only in areas of the islands with a relatively recent pahoehoe-like basaltic volcanism. This explains the lack of tubes in the islands of La Gomera and their scarcity in Gran Canaria and most of Fuerteventura. However, even in the absence of caves, a very rich underground environment, in the form of shallow, intermediate-sized, interconnected voids, is present in all the islands.

Before the present study 29 endemic species of *Dysdera* had been reported from Tenerife, by far the most species-rich island in the archipelago. These species were: *D. ambulotenta* Ribera et al. 1985 (♂, ♀; one locality); *D. brevisetae* Wunderlich 1991 (♂, single specimen); *D. brevispina* Wunderlich 1991 (♂, single specimen); *D. chioensis* Wunderlich 1991 (♀, one locality); *D. cribellata* Simon 1883 (♂, ♀); *D. curvisetae* Wunderlich 1987 (♂, single specimen); *D. esquiveli* Ribera & Blasco 1986 (♂, ♀); *D. gibbifera* Wunderlich 1991 (♂, ♀); *D. gollumi* Ribera & Arnedo 1994 (♀, one locality); *D. iguanensis* Wunderlich 1987 (♂, ♀); *D. inaequuscapillata* Wunderlich 1991 (♂, ♀); *D. insulana* Simon

1883 (♂, ♀; one locality); *D. labradaensis* Wunderlich 1991 (♀, one locality); *D. levipes* Wunderlich 1987 (♂, ♀); *D. medinae* Wunderlich 1991 (♂, ♀); *D. minutissima* Wunderlich 1991 (♂, single specimen); *D. montanetensis* Wunderlich 1991 (♂, single specimen); *D. moquinalensis* Wunderlich 1991 (♂, single specimen); *D. obscuripes* Wunderlich 1991 (♂, ♀); *D. pergrada* Wunderlich 1991 (♂, ♀; one locality); *D. propinqua* Ribera et al. 1985 (♂, single specimen); *D. pseudopergrada* Wunderlich 1991 (♂, ♀); *D. rugichelis* Simon 1907 (♂, single specimen in Tenerife); *D. taibaensis* Wunderlich 1991 (♂, single specimen); *D. teideensis* Wunderlich 1991 (♂, ♀); *D. teneriffensis* Strand 1908 (♀; single specimen, lost); *D. unguimmanis* Ribera et al. 1985 (♀, single specimen); *D. vilaflorensis* Wunderlich 1991 (♂, single specimen) and *D. volcania* Ribera et al. 1985 (♂, ♀; one locality) (Bösenberg 1895; Strand 1908; Denis 1941, 1953; Schmidt 1975; Ribera et al. 1985; Wunderlich 1987, 1991; Ribera & Arnedo 1994; Arnedo et al. 1996; Arnedo & Ribera 1997). Six of these species displayed morphological adaptations to the hypogean environment and were considered to be true troglobites. With a single exception (*Dysdera ratonensis* Wunderlich 1991 from La Palma), the lava tubes of Tenerife hold all troglomorphic *Dysdera* documented so far in the Canaries.

METHODS

The current study was based on the adoption of the so-called 'diagnosability' (Baum 1992) phylogenetic species concept (Nixon & Wheeler 1990, 1992; Wheeler & Nixon 1990, Davis & Nixon 1992). Species are recognized as the most exclusive set of populations that display a unique combination of character-states, when semaphoronts are compared (Davis & Nixon 1992). This concept was selected because it is easily applicable in practice, it avoids any reference to processes, and is fully compatible with a phylogenetic framework. However, this definition is not free of theoretical problems (Frost & Kluge 1994) and has been considered to be excessively restrictive. In addition, in the present approximation, only morphological characters were taken into account, which has probably resulted in an underestimation of the total number of species. Additional studies considering molecular, eco-

logical or behavioral characters would be necessary in order to recover the total amount of diversity of the genus.

The first stage in the assessment of the taxonomic status of the Tenerifean species was to gather a large number of specimens (350), which were made available from scientific institutions, various personal collections, and three collection expeditions to the island by the authors. The following colleagues and museum kindly supplied material for the present study: Dr. E. Enghoff from the Zoologisk Museum of Copenhagen (ZMK), R. García 'Felo' (S/C de la Palma, Canary Islands) (RG), F. Gasparo (Trieste, Italy) (FG), Mr. P.D. Hilliard from the Natural History Museum of London (BMNH), Dr. M. Grasshoff from the Forschungsinstitut und Naturmuseum Senckenberg (SMF), Dr. P. Oromí from the Universidad de La Laguna (UL), Dr. G. Ortega from the Museo de Ciencias Naturales de Santa Cruz de Tenerife (MCNT), Dr. C. Rollard from the Muséum National d'Histoire Naturelle de Paris (MNHN) and J. Wunderlich (Straubenhardt, Germany) (JW). The material provided by the authors' expeditions is stored at the collection of Arachnids of the University of Barcelona, Spain (UB).

Characters were investigated under a Wild Heerbrugg (12–100 \times) dissecting microscope. Female vulva (= endogyne, Mcheidze 1972) was removed and muscle tissues digested using a KOH (35%) solution before observation. Male bulbi and spinnerets were removed, cleaned by means of ultrasound and examined using a HITACHI S-2300 scanning electron microscope at 10–15 Kv. All measurements are in millimeters. Somatic morphology measurements were taken using an ocular micrometer in the dissecting microscope. Characters examined together with their diagnostic resolution have been discussed elsewhere (Arnedo et al. 1996). All characters were recorded in DELTA format (Dallwitz 1980; Dallwitz et al. 1993).

Terminology.—Leg spination was recorded for each segment using the format of Arnedo et al. (1996). Only spines present on femorae, patellae and tibiae were considered. In femora, spines are usually arranged in one or two (anterior and posterior) rows parallel to the segment. The number of rows and spines per row were recorded (In Tables 2–16, the number of spines in each row were separated

by a slash). In patellae, the number of spines and their position (ventral or dorsal) was coded. Tibiae usually show the most complex spination pattern. For each tibia, the number of spines was recorded from four zones (hereafter referred as 'bands'): proximal, medial-proximal, medial-distal and distal. For coding purposes, the number of spines on the frontal, medial and posterior regions were separated by points. In the descriptions (intra-individual variation), hyphens separate the number of spines on each side of the body if different. In the tables (intraspecific variation) hyphens separate the minimum and maximum number of spines observed in any specimen. Between 6–10 individuals were examined from each species whenever possible.

Structures of male bulb and female vulva were mostly named after Deeleman-Reinhold & Deeleman (1988), with the addition of several features particular to Canarian *Dysdera* (Arnedo et al. 1996; Arnedo & Ribera 1997). Nevertheless, some new characters from the female vulva have been added or have been redefined and deserve further considerations. The vulva of the genus *Dysdera* is divided into two major diverticles: an anterior diverticle and a posterior one. They are separated by the epigastric furrow at the ventral side, and the oviduct opening at the dorsal one. The posterior diverticle is mostly membranous, with the single exception of the transversal bar. This is located at the anterior dorsal side and holds a frontal projection ('bursal valve', V) that closes the oviduct openings. On the other hand, most of the anterior diverticle is usually sclerotized. The most conspicuous structure is a T-shaped spermatheca (S) located at the ventral side of the most anterior margin. The medial lateral margins of the anterior diverticle are invaginated forming two different pouches: a dorsal pouch, which corresponds to the so-called 'dorsal arch' (DA) (Deeleman-Reinhold & Deeleman 1988) and a ventral one, hereafter referred as 'ventral arch' (VA). The DA is usually completely sclerotized. The dorsal side of the DA locks the V and is called the 'dorsal fold' (DF) (Arnedo et al. 1996). The fold that separates both diverticles is named the 'major fold' (MF), to differentiate it from several additional folds that are sometimes found on the DA lateral borders. The development and sclerotization degree of the MF are highly variable. In some

Table 1.—Abbreviations used in text and figures (Figs. 4–12).

<i>Female genitalia</i>	<i>Male copulatory bulb</i>
DA = dorsal arch	T = tegulum
DF = dorsal fold	DD = distal division
MF = major fold	IS = internal sclerite
S = spermatheca	ES = external sclerite
TB = transversal bar	DH = distal haematodoca
V = bursal valve	C = crest
VA = ventral arch	AC = additional crest
AVD = additional ventral diverticle	LF = lateral fold over L, between internal and external sclerites
<i>Eyes</i>	L = lateral sheet
AME = anterior medial eyes	AL = additional lateral sheet at back internal border
PME = posterior medial eyes	P = posterior apophysis
PLE = posterior lateral eyes	
<i>Chelicerai teeth</i>	<i>Spinnerets</i>
B = basal tooth	ALS = anterior lateral spinnerets
M = medial tooth	PMS = posterior medial spinnerets
D = distal tooth	PLS = posterior lateral spinnerets
	MS = major ampulate gland spigot
	PS = polar pyriform gland spigot

continental *Dysdera* species, the MF almost entirely isolates the DA from the VA. The margins of the MF may be markedly separated from each other or stuck together forming an internal rim. The VA exhibits a wide range of sclerotization levels, from mostly sclerotized to completely membranous. In most of the Canarian representatives, an additional ventral diverticle (AVD) in the VA has been observed. The AVD is recognized by an internal rim ventral to the MF and by its own external sclerotization, usually tooth shaped. Spinnerets and their associated spigot glands were assigned after Platnick et al. (1991). See Table 1 for a complete list of abbreviations.

FAMILY DYSDERIDAE

Genus *Dysdera* Latreille 1804

Note: An excellent and thorough diagnosis and description of the genus *Dysdera* can be

found in Deeleman-Reinhold & Deeleman (1988).

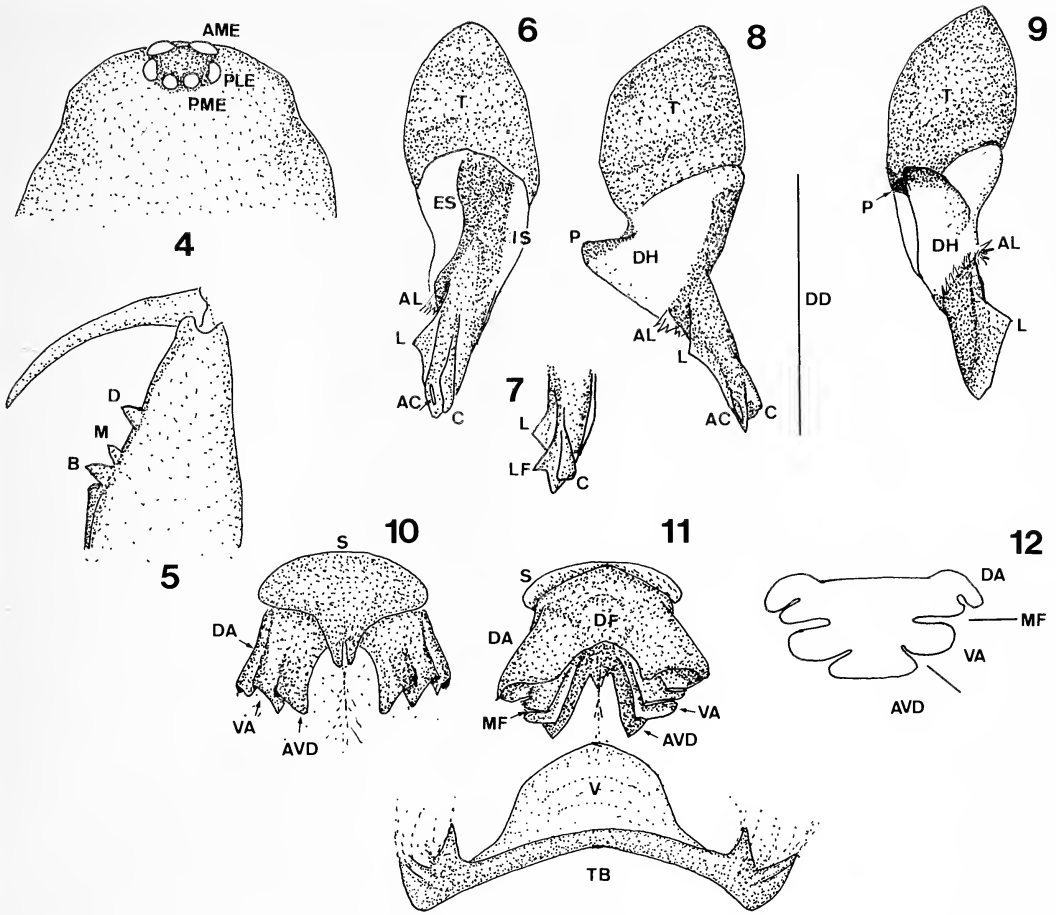
Dysdera ambulotenta Ribera, Ferrández & Blasco 1985
Figs. 13–24, Table 2

Dysdera ambulotenta Ribera, Ferrández & Blasco 1985: 54–57, fig. 1 [♂, ♀]. Holotype male and paratype female (allotype) from Cueva del Viento-Sobrado, El Amparo, Icod de los Vinos, Tenerife, Canary Islands; 14 May 1981, J.L. Martín leg.; ♂ (T-CS-17), ♀ (T-CS-18). Stored at UL. Examined. Wunderlich 1991: 284–287.

Diagnosis.—*Dysdera ambulotenta* can be distinguished from all other Canarian *Dysdera* species, except *D. labradaensis*, by its large size (carapace > 6.5 mm) and remarkable eye reduction. It differs from *D. labradaensis* (male unknown) by complete absence of both the posterior lateral (PLE) and posterior me-

Table 2.—Intraspecific spination variability of *Dysdera ambulotenta*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.0-2.1	1.0-2.0-1	0	1.0.1
Tibia 4 dorsal	0-1.0.0-1	1.0-3.1	0-1.0-3.0-1	1.0.1
Tibia 3 ventral	1.1-3.1	1.1-2.1	0	1.0.0-1
Tibia 4 ventral	1.1-2.1	1.1-2.1	0-2.0-2.1-2	0-1.0-2.1
	Number of rows		Number of spines	
Femur 3 dorsal	2		0-3/0-1	
Femur 4 dorsal	2		0-4/0-4	



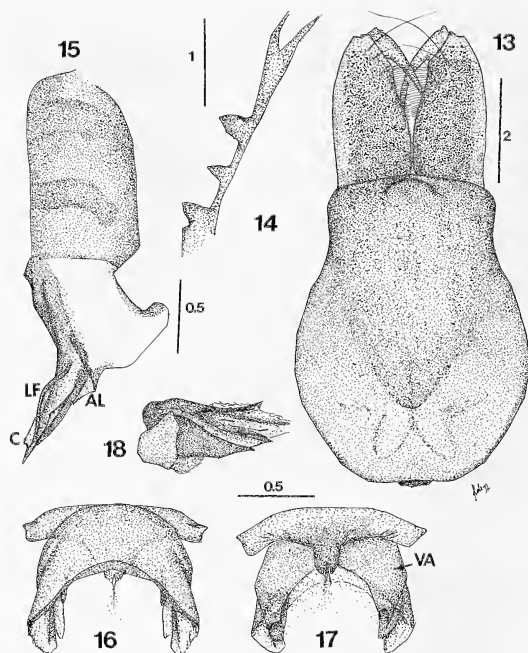
Figures 4–12.—Diagrams showing the characters included in the abbreviations list (Table 1). 4, Carapace frontal region, dorsal view; 5, Left chelicera, ventral view; 6, Right bulb, frontal view; 7, Right bulb distal tip, frontal view; 8, Bulb, external view; 9, Bulb, posterior view; 10, Vulva, ventral view; 11, Vulva, dorsal view; 12, Vulva, transverse section.

dial eyes (PME), lack of spines on legs 1 and 2 and absence of an additional ventral diverticle (AVD) in the vulva (Fig. 17). In both sexes absence of a polar spigot (PS) in the anterior lateral spinnerets (ALS) is unique to this species (Fig. 23).

Description.—*Holotype male*: Figs. 13–15, 19–22. Carapace (Fig. 13) 7.35 mm long; maximum width 5.6 mm; minimum width 3.78 mm. Reddish-orange, frontally darker, becoming lighter towards back; slightly foveate at borders, slightly wrinkled with a fine-textured granular surface primarily at the anterior end. Frontal border roughly straight, from $\frac{1}{2}$ to $\frac{3}{5}$ carapace length; anterior lateral borders convergent (backwards long, parallel); rounded at maximum dorsal width point, back lateral borders rounded; back margin wide,

straight PME, PLE lost; AME markedly reduced; AME diameter 0.09 mm; AME separation 0.936 mm. Labium trapezoid-shaped, base wider than distal part; longer than wide at base; semicircular groove at tip. Sternum dark orange, frontally darker, becoming lighter towards back; very slightly wrinkled, mainly between legs, frontal border; uniformly covered in slender black hairs.

Chelicerae (Fig. 14) 4.41 mm long, about $\frac{2}{5}$ of carapace length in dorsal view; fang medium-sized, 2.8 mm; basal segment dorsal side completely covered with piligerous granulations (small, densely), ventral side smooth. Chelicera inner groove medium-size, about $\frac{2}{5}$ cheliceral length; armed with three teeth and lamina at base; $D > B > M$ (large teeth; D, B not very different); D round, located rough-



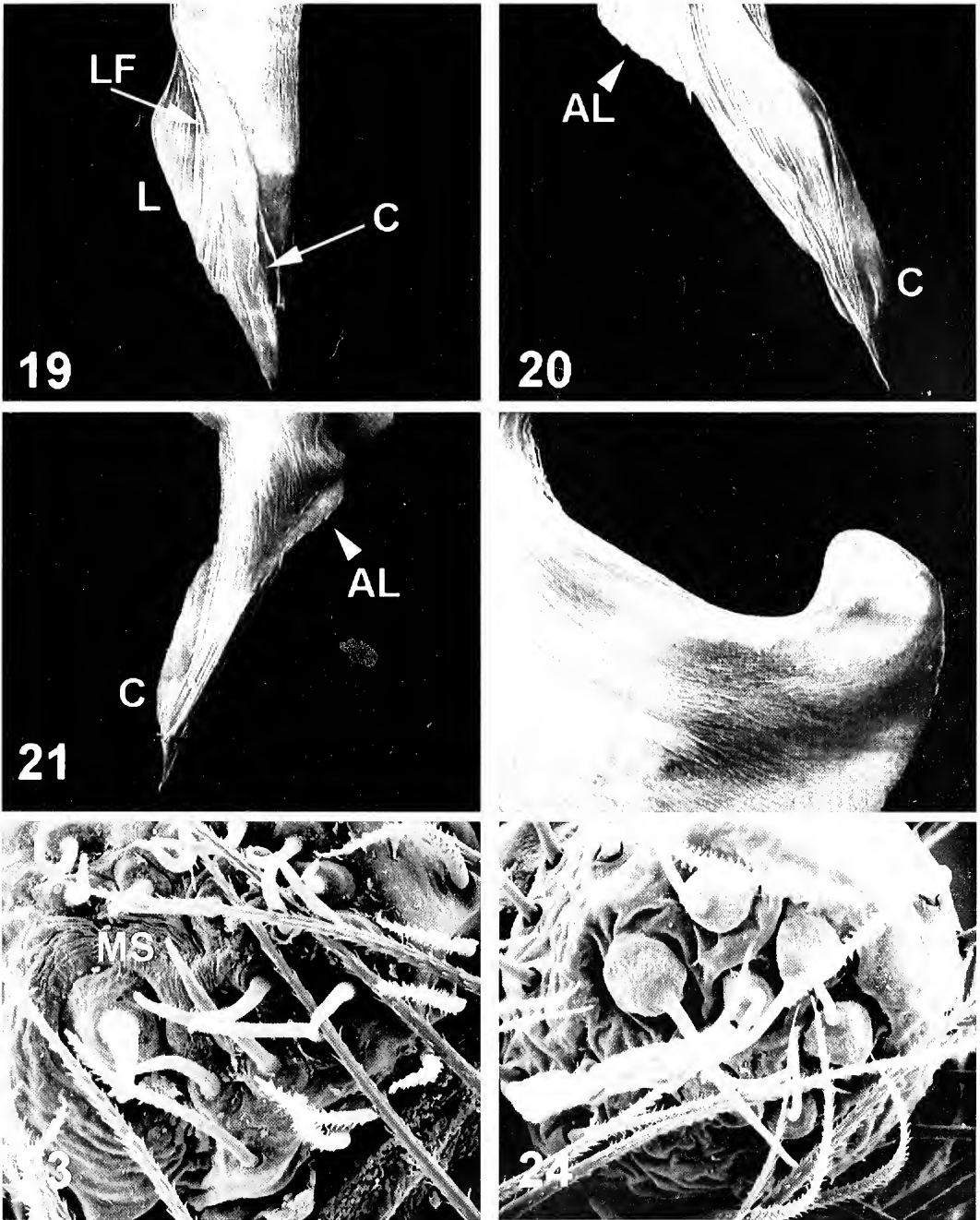
Figures 13–18.—*Dysdera ambulotenta*. 13, Carapace, dorsal; 14, Left chelicera, ventral; 15, Left male bulb, external; 16, Vulva, dorsal; 17, Vulva, ventral; 18, Vulva, lateral. Scale bars in mm.

ly at center of groove; B close to basal lamina; M at middle of B and D. Legs orange. Lengths of male described above: fe1 6.6 mm (all measurements in mm); pa1 4.3; ti1 6.3; me1 5.4; ta1 1.2; total 23.8; fe2 6.3; pa2 4; ti2 6.2; me2 5.2; ta2 1.2; total 22.9; fe3 5.2; pa3 2.9; ti3 3.8; me3 4.5; ta3 1.3; total 17.7; fe4 6.3; pa4 3.4; ti4 5.3; me4 6; ta4 1.4; total 22.4; relative length: $1 > 2 > 4 > 3$; palp: fe 3.5; pa 2; ti 2; ta 1.9; total 9.4. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spines in two rows: anterior 3 (distal); posterior 1 (proximal); ti3 dorsal spines arranged in three bands: proximal 1.2-1; medial-proximal 1.1-2.1; distal 1.0-1; ti3 ventral spines arranged in three bands: proximal 1-0.3-2.1; medial-proximal 1.3-2.1; distal 1.0-1; with two terminal spines. Fe4 dorsal spines in two rows: anterior 4-2; posterior 3-2; ti4 dorsal spines arranged in four bands: proximal 1-0.0-1-0; medial-proximal 1.2-1; medial-distal 1.3-2.1; distal 1.0-1; ti4 ventral spines arranged in four bands: proximal 1.2-1.1; medial-proximal 1.2-1; medial-distal 1.2-1.1; distal 1.1-0.1; with two terminal spines. Dorsal side of frontal legs with a fine-textured piligerous granular surface; ventral side of palp smooth; posterior legs

densely covered with short hairs. Claws with more than 15 teeth, slender, length twice claw width. Abdomen 10.5 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.027 mm long (short); medium-sized, roughly straight, not compressed, blunt, tip enlarged; uniformly, thickly distributed.

Male bulb (Fig. 15): T as long as DD; external distal border straight; internal sloped backwards. DD bent about 45° in lateral view; internal distal border not expanded. ES wider, more sclerotized than IS; IS continuous to tip. DD tip (Figs. 19–21) straight in lateral view. C present, long; distal end on DD internal tip; well-developed; located far from DD distal tip; proximal border continuously decreasing; distal border markedly sloped, upper tip not projected, pointed; external side hollowed. AC absent. LF present; distally not projected; poorly developed. L well-developed; external border not sclerotized, laterally slightly folded, distal border divergent, continuous. AL present, well-developed; proximal border in posterior view fused with DH. P (Fig. 22) fused to T; markedly sloped on its proximal part, perpendicular on distal; lateral length as long as or longer than T width; ridge present, perpendicular to T, not expanded; upper margin smooth; not distally projected; back margin not folded.

Paratype female: Figs. 16–18, 23, 24. All characters as in male except: Carapace 7.21 mm long; maximum width 5.6 mm; minimum width 3.64 mm. AME separation 1.16 mm. Chelicerae 4 mm long; fang 3.22 mm. Legs orange. Lengths of female described above: fe1 6.6 mm (all measurements in mm); pa1 4.3; ti1 6.2; me1 5.4; ta1 1.3; total 23.8; fe2 6.1; pa2 4.1; ti2 6.1; me2 5.4; ta2 1.3; total 23; fe3 5.2; pa3 3; ti3 3.9; me3 4.8; ta3 1.2; total 18.1; fe4 6.5; pa4 3.5; ti4 5.2; me4 6.3; ta4 1.5; total 23; relative length $1 > 2 = 4 > 3$; palp: fe 4; pa 2; ti 1.9; ta 2.5; total 10.4. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spines in two rows: anterior 2; posterior 1; ti3 dorsal spines arranged in three bands: proximal 1.0-1; medial-proximal 1.0-1; distal 1.0-1; ti3 ventral spines arranged in three bands: proximal 2-1.2-2-1; medial-proximal 1.3-1.0-1; distal 1.0-1; with two terminal spines. Fe4 dorsal spines in two rows: anterior 1; posterior 2; ti4 dorsal spines arranged in four bands: proximal 1-0.0-1-0; medial-proximal 1.2-0.1; medial-distal 1.3-1.1; distal



Figures 19–24.—*Dysdera ambulotenta*, right male bulb and female spinnerets. 19, DD frontal; 20, DD external; 21, DD internal; 22, P internal view; 23, Right ALS; 24, Right PLS.

1.0.0; ti4 ventral spines arranged in four bands: proximal 1.1.1; medial-proximal 1.1-2.1; medial-distal 0-1.1-0.1; distal 0-1.1-0.1; with two terminal spines.

Abdomen 7 mm long. Abdominal dorsal hairs 0.036 mm long (short); medium thick-

ness, roughly straight, not compressed, blunt, tip enlarged; uniformly, thickly distributed. Vulva (Figs. 16–18) rectangle-like in dorsal view, frontally rounded; slightly wider than long; DF wide. MF well-developed; markedly sclerotized along its extent. VA frontal region

completely sclerotized; posterior region sclerotized except for internal area. AVD absent. S attachment projected under VA; arms as long as DA, slightly curved; tips dorsally projected; neck as wide as arms. TB usual shape. ALS (Figs. 23–24) without PS; remaining piriform spigots no more external than MS, arranged in three rows; 18 piriform gland spigots; PMS, PLS with 5–10 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 7.00–7.35 mm, female from 6.51–7.00 mm. Sometimes carapace lateral margin angled at maximum width point. AME reduction variable, from tiny bright spots to absent. Chelicera relative length from 0.43–0.48. D as large as or slightly larger than B. One male from Los Roques with M distinctly closer to D. In general, cheliceral teeth are large. Spination variability in Table 2.

Additional material examined.—**TENERIFE:** *El Sauzal:* Cueva de Labrada-Mechas, 13 March 1982, 1♂ subadult (J.L. Martín, num. 2520 UL). *Icod de los Vinos:* Cueva de Felipe Reventón, 17 March 1984, some remains (J.J. Hernández, num. 2534 UL). Cueva del Viento-Sobrado, 10 December 1982, 1juv. (J.L. Martín, num. 2517 UL); 2 November 1991, 1juv. (J.L. Martín, num. 2518 UL). *La Orotava:* Cueva del Bucio, 27 November 1984, some remains (J.L. Martín & A. Machado, num. 2794 UL); 4 March 1985, 1juv. (J.L. Martín & A. Machado, num. 2532 UL). 1 April 1991, 1♀ (Lucas & Rando, num. 2511 UL). Cueva de los Roques, 11 August 1986, 1♂ (J.L. Martín, num. 2512 UL); 27 October 1991, ? (one chelicera) (C. Ribera, num. 2568 UL); 25 September 1996, 1♀ (P. Oromí, num. 3184 UB).

Distribution.—Tenerifean endemic. Exclusively known from lava tubes. It is the most widespread of troglomorphic *Dysdera*.

Dysdera brevisetae Wunderlich 1991

Figs. 25–36

Dysdera brevisetae Wunderlich 1991: 289–290, fig. 14–16 [♂]. Holotype male from Monte de las Mercedes, La Laguna, Tenerife, Canary Islands; in II, M. Knösel leg.; num. 37166. Stored at SMF. Examined. —Wunderlich 1991: 284–287.

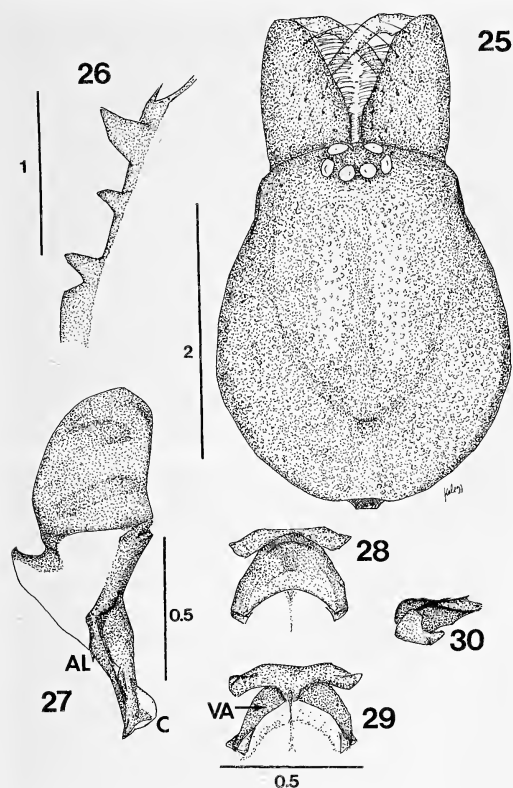
Diagnosis.—*Dysdera brevisetae* is distinguished from any other markedly foveate species by its wider carapace frontal border and spineless femora and tibiae. Males differ from the morphologically similar *D. macra* by a

poorly developed but complete bulb lateral sheet (L) (Fig. 31), and both males and females have anterior medial eyes separated by less than $\frac{2}{3}$ of its diameter from each other, longer chelicera inner groove and cheliceral distal tooth (D) markedly larger than basal one (B) (Fig. 26).

Description.—*Holotype male:* Figs. 25–27, 31–34. Carapace (Fig. 25) 3.62 mm long; maximum width 2.51 mm; minimum width 1.84 mm. Dark red, darkened at borders; heavily wrinkled, foveate, with a fine-textured granular surface. Frontal border roughly round, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders parallel or slightly divergent; rounded at maximum dorsal width point, back lateral borders rounded; back margin narrow, straight; slightly stepped in lateral view. AME diameter 0.21 mm; PLE 0.21 mm; PME 0.16 mm; AME on edge of frontal border, separated one from another about $\frac{1}{2}$ of diameter, close to PLE; PME very close to each other, less than $\frac{1}{4}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; as long as wide at base (triangle-like); semi-circular groove at tip. Sternum brownish-red, darkened on borders; heavily wrinkled; uniformly covered in slender black hairs.

Chelicerae (Fig. 26) 1.58 mm long, about $\frac{2}{5}$ of carapace length in dorsal view; fang long, 1.35 mm; basal segment dorsal, ventral side completely covered with piligerous granulations. Chelicera inner groove long, about $\frac{1}{2}$ cheliceral length; armed with three teeth and lamina at base; D > B = M (B, M small); D trapezoid, located near segment tip; B close to basal lamina; M close to D. Legs orange. Lengths of male described above: fe1 2.4 mm (all measurements in mm); pa1 1.44; ti1 2.14; me1 2; ta1 0.51; total 8.49; fe2 2.23; pa2 1.35; ti2 1.91; me2 1.98; ta2 0.51; total 7.98; fe3 1.79; pa3 1.07; ti3 1.26; me3 1.68; ta3 0.51; total 6.31; fe4 2.19; pa4 1.12; ti4 1.82; me4 2; ta4 0.53; total 7.66; relative length: 1 > 2 > 4 > 3; palp: fe 1.4; pa 0.74; ti 0.74; ta 0.74; total 3.62. Spination: spineless. Dorsal side of frontal legs covered with hairs, lacking a granular surface; ventral side of palp smooth; long, spine-like hairs on posterior ti, fe. Claws with 10–14 teeth, length twice claw width.

Abdomen 3.73 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.045 mm long; medium thickness, roughly straight, not com-



Figures 25–30.—*Dysdera brevisetae*. 25, Carapace, dorsal; 26, Left chelicera, ventral; 27, Right male bulb, external; 28, Vulva, dorsal; 29, Vulva, ventral; 30, Vulva, lateral. Scale bars in mm.

pressed, blunt, tip enlarged; uniformly, thickly distributed.

Male bulb (Fig. 27): T slightly smaller than DD; external, internal distal border sloped backwards. DD slightly bent in lateral view, clearly less than 45° ; internal distal border not expanded. IS, ES equally developed; IS truncated at DD middle part; ES bend markedly sclerotized. DD tip (Figs. 31–33) straight in lateral view. C present, short; distal end on DD internal tip; well-developed; located close to DD distal tip; proximal border sharply decreasing; distal border rounded, hardly stepped, upper tip not projected, rounded; external side hollowed. AC present. LF absent. L poorly developed; external border not sclerotized, laterally slightly folded; distal border divergent, not continuous; upper sheet strongly folded at middle. AL present, very poorly developed; proximal border in posterior view fused with DH. P (Fig. 34) fused to T; per-

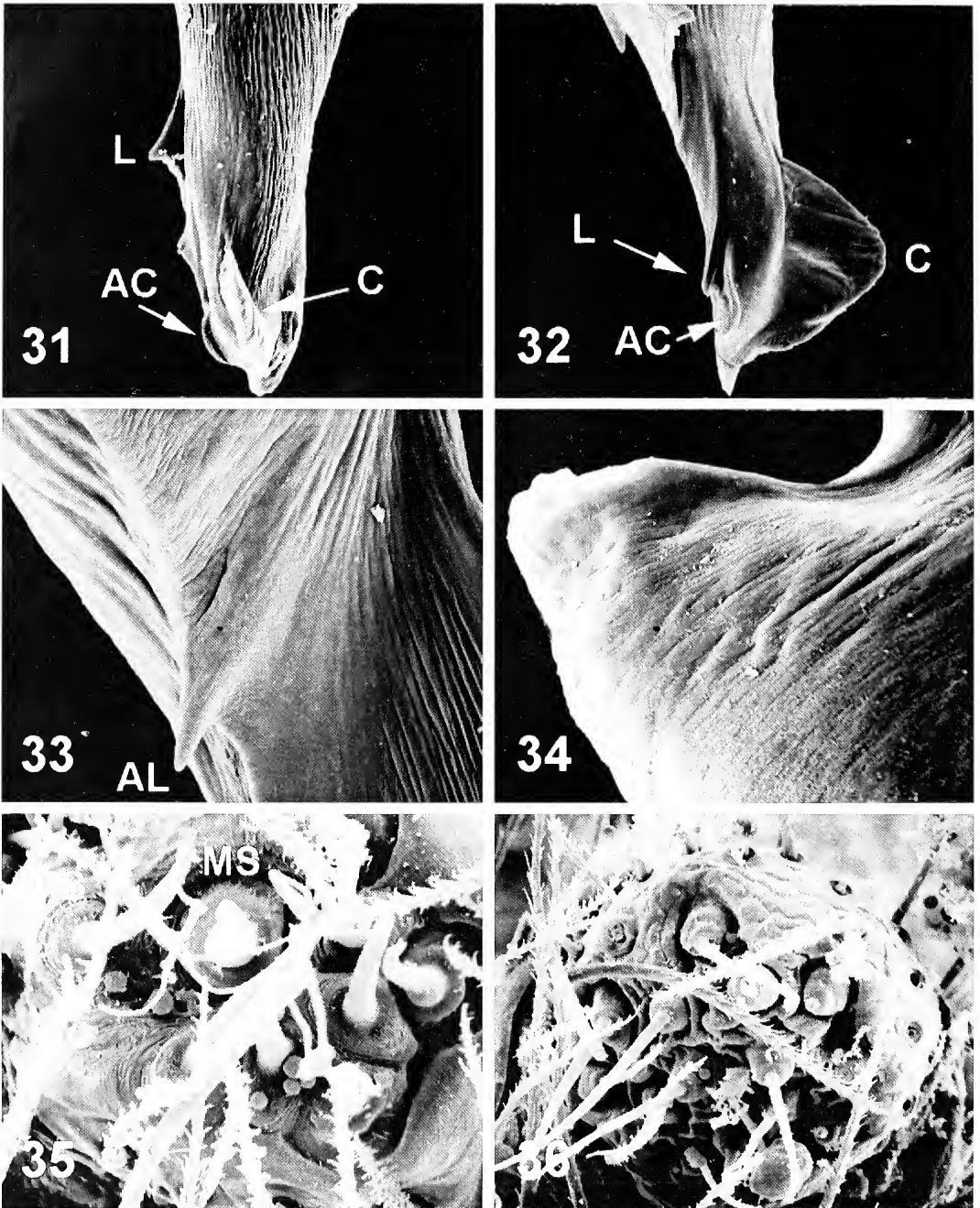
pendicular to T in lateral view; lateral length from $\frac{1}{3}$ – $\frac{2}{5}$ of T width; ridge present, perpendicular to T, not expanded; upper margin smooth; not distally projected; back margin slightly folded towards internal side.

Female: (from El Moquinal, La Orotava, Tenerife; num. 2935, UB) Figs. 28–30, 32, 33. All characters as in male except: Carapace 3.66 mm long; maximum width 2.65 mm; minimum width 1.98 mm. AME diameter 0.23 mm; PLE 0.2 mm; PME 0.16 mm. Sternum dark red. Chelicerae 1.72 mm long; fang 1.4 mm; basal segment proximal dorsal, ventral side scantily covered with piligerous granulations. Legs orange. Lengths of female described above: fe1 2.42 mm (all measurements in mm); pa1 1.54; ti1 2.1; me1 2.05; ta1 0.53; total 8.64; fe2 2.25; pa2 1.44; ti2 1.91; me2 2; ta2 0.53; total 8.13; fe3 1.91; pa3 1.26; ti3 1.38; me3 1.68; ta3 0.51; total 6.56; fe4 2.28; pa4 1.26; ti4 1.91; me4 2.1; ta4 0.53; total 8.08; relative length $1 > 2 > 4 > 3$; palp: fe 1.4; pa 0.79; ti 0.56; ta 0.88; total 3.63.

Abdomen 4.66 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.16–0.18 mm long; thin, curved, compressed, pointed; uniformly, thickly distributed. Vulva (Figs. 28–30) arch-like in dorsal view, frontally rounded; slightly wider than long; DF wide. MF poorly developed. VA frontal region completely sclerotized; posterior region sclerotized at anterior area. AVD hardly visible. S attachment not projected under VA; arms as long as DA, slightly curved; tips dorsally projected; neck as wide as arms. TB usual shape. ALS (Figs. 32–33) with PS; remaining piriform spigots more external than MS, arranged in two rows; 7 + 1 piriform gland spigots; PMS, PLS with 5–10 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 3.62–3.54 mm, female from 3.40–3.66 mm. PLE-PME from $\frac{1}{5}$ – $\frac{2}{5}$ diameter. Sternum ornamentation somewhat reduced. B may be larger than M. M sometimes closer to B.

Additional material examined.—**TENERIFE:** *La Laguna:* Cocomoto, ? February 1989, 1♂ (C. Deniz, num. 2680 UL). El Moquinal, under a bark of *Erica scoparia*, 18 October 1994, 1♀ (P. Oromí, num. 4001 UB). Monte de las Mercedes, 30 January 1989, 1♂ (H. Enghoff, num. 2640 ZMK). *Los Silos:* Monte del Agua, 14 March 1987, 1juv. (H. Enghoff, num. 2669 ZMK); 1 February 1988, 1♀ (J.J. Naranjo, num. 2598 UB); 3 March 1989, 1♀



Figures 31–36.—*Dysdera brevisetae*, right male bulb and female spinnerets. 31, DD frontal; 32, DD external; 33, DD posterior; 34, P external; 35, Right ALS; 36, Right PLS.

(H. Enghoff & M. Baez, num. 2646 ZMK); 3 March 1989, 1♀ (H. Enghoff, num. 2659 ZMK); 18 February 1996, ljuv. (Arnedo & Oromí, num. 3118 UB). *Santa Cruz de Tenerife*: Bailadero, ? November 1993, 1♀ (Arnedo & Ribera, num. 4784 (T21) UB). Cabezo de Tejo, 26 February 1996, 1♀

(Oromí & Emerson, num. 3128 UB). Casas de la Cumbre, 23 February 1996, ljuv. (Oromí & Emerson, num. 3127 UB). Cruz del Carmen, 12 May 1996, 1♂ (M. Naranjo, num. 3145 UB). Vueltas de Taganana, 20 February 1984, 1♂ (García Alayón, num. 2687 UL); May 1995, 1♂ (P. Oromí, num.

Table 3.—Intraspecific spination variability of *Dysdera brevispina*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	0-1.0-2.1	0	0	1.0.0
Tibia 4 dorsal	1.1-2.1	0	0	1.0-1.1
Tibia 3 ventral	0-1.1-.2.0-1	0	0	1.0.0
Tibia 4 ventral	12-.3.0-1	0	0	1.0.0-1
	Number of rows		Number of spines	
Femur 3 dorsal	0		0	
Femur 4 dorsal	1		0-1	

4181 UB). 29 November 1996, 1 ♀ (P. Oromí, num. 3189 UB). *Tegueste*: Pedro Alvarez, 19 February 1997, 1 ♂ (B. Emerson, num. 3204 UB; 20 February 1997, 1 ♂, (P. Oromí, num. 3205 UB).

Distribution.—Tenerifean endemic. Abundant species known from several localities restricted to Anaga and Teno massifs.

Comments.—Originally known from a single male specimen, this species has been extensively collected in Tenerife.

Dysdera brevispina Wunderlich 1991
Figs. 37–48, Table 3

Dysdera brevispina Wunderlich 1991: 289–290, figs. 17–19 [♂]. Holotype male from Cueva de Felipe Reventón, Icod de los Vinos, Tenerife, Canary Islands; 23 March 1984, A. Machado leg.; num. T-FR-97. Stored at UL. Examined. -Wunderlich 1991: 284–287.

D. moquinalensis Wunderlich 1991: 301, figs. 65–68 [♂]. El Moquinal, La Laguna, Tenerife, Canary Islands; 1 ♂; 20/4/90, P. Oromí leg.; Stored at UL. Examined. New synonymy.

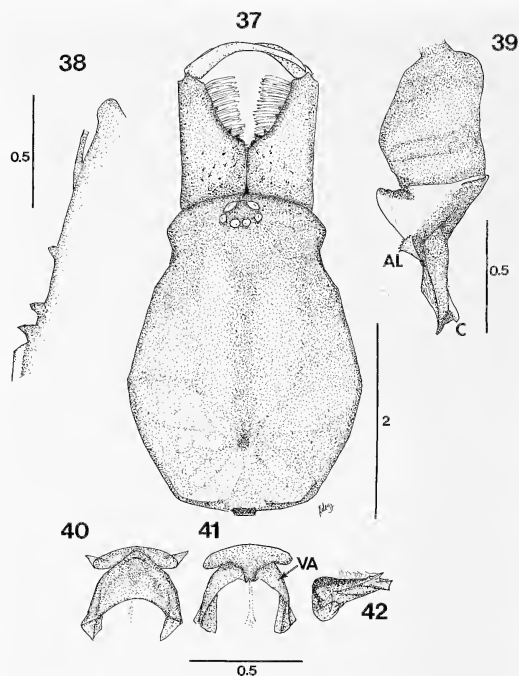
D. vilaflorensis Wunderlich 1991: 310–311, figs. 124–125 [♂]. MSS-6, Barranco del Chorrillo, Vilaflo, Tenerife, Canary Islands; 1 ♂; 15 May 1990, A.L. Medina leg.; Stored at UL. Examined. New synonymy.

Diagnosis.—*Dysdera brevispina* is distinguished from most of the Canarian *Dysdera* species by its smooth carapace and by the cheliceral basal tooth (B) being the largest (Fig. 38). Males and females differ from the eastern Canary Islands endemics by lack of thick and lanceolate abdominal hairs, from *D. chioensis* and *D. unguimmanis* by absence of eye reduction and from from *D. guayota* new species by absence of spines on frontal legs. Males distinguished from *D. insulana* by lacking medial fold in bulb lateral sheet (L) (Fig. 43), and both males and females by presence

of cheliceral granulation and distinctive spination pattern (Table 3).

Description.—*Holotype male*: Figs. 37–39, 43–47. Carapace (Fig. 37) 3.63 mm long; maximum width 2.7 mm; minimum width 1.68 mm. Brownish-orange, darkened at borders; slightly foveate at borders, slightly wrinkled and a black fine-textured granular surface mostly at the anterior end. Frontal border roughly round, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders slightly convergent; rounded at maximum dorsal width point, back lateral borders straight; back margin wide, straight. AME diameter 0.16 mm; PLE 0.14 mm; PME 0.12 mm; AME on edge of frontal border, separated one from another about 1 diameter or more, close to PLE; PME very close to each other, about $\frac{1}{2}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base; semicircular groove at tip. Sternum brownish-orange, darkened on borders; very slightly wrinkled, mainly between legs, frontal border; uniformly covered in slender black hairs.

Chelicerae (Fig. 38) 1.56 mm long, about $\frac{2}{5}$ of carapace length in dorsal view; fang long, 1.35 mm; basal segment proximal dorsal side scanty covered with piligerous granulations. Chelicera inner groove medium-size, about $\frac{2}{5}$ cheliceral length; armed with three teeth, lamina at base; additional tooth on left chelicera; $B > D = M$ (D, M markedly small); D triangular, located roughly at center of groove; B close to basal lamina; M close to B. Legs pale yellow. Lengths of male described above: fe1 3.45 mm (all measurements in mm); pa1 2.19; ti1 3.12; me1 2.93; ta1 0.6; total 12.29; fe2 3.03; pa2 1.96; ti2 2.79; me2 2.7; ta2 0.6; total 11.08; fe3 3.12; pa3 1.4; ti3 1.72; me3 2.23; ta3 0.56; total 9.03; fe4 3.68; pa4 1.86;



Figures 37–42.—*Dysdera brevispina*. 37, Carapace, dorsal; 38, Left chelicera, ventral; 39, Right male bulb, external; 40, Vulva, dorsal; 41, Vulva, ventral; 42, Vulva, lateral. Scale bars in mm.

ti4 2.65; me4 3.26; ta4 0.65; total 12.1; relative length: $1 > 4 > 2 > 3$; palp: fe 1.72; pa 0.84; ti 0.93; ta 0.93; total 4.42. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.1–0.1; distal 1.0–0; ti3 ventral spines arranged in two bands: proximal 2–1.3–0.2–1; distal 1.0–1.1; with two terminal spines. Fe4 dorsal spineless; ti4 dorsal spines arranged in two bands: proximal 1.1–0; distal 1.0–0; ti4 ventral spines arranged in two bands: proximal 1.3–2.0; distal 1.0–0; with two terminal spines. Dorsal side of frontal legs smooth; ventral side of palp covered with hairs, lacking small a granular surface. Claws with 10–14 teeth; hardly larger than claw width.

Abdomen 4.52 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.018–0.027 mm long (small); medium thickness, roughly straight, not compressed, blunt, tip not enlarged; uniformly, scantily distributed.

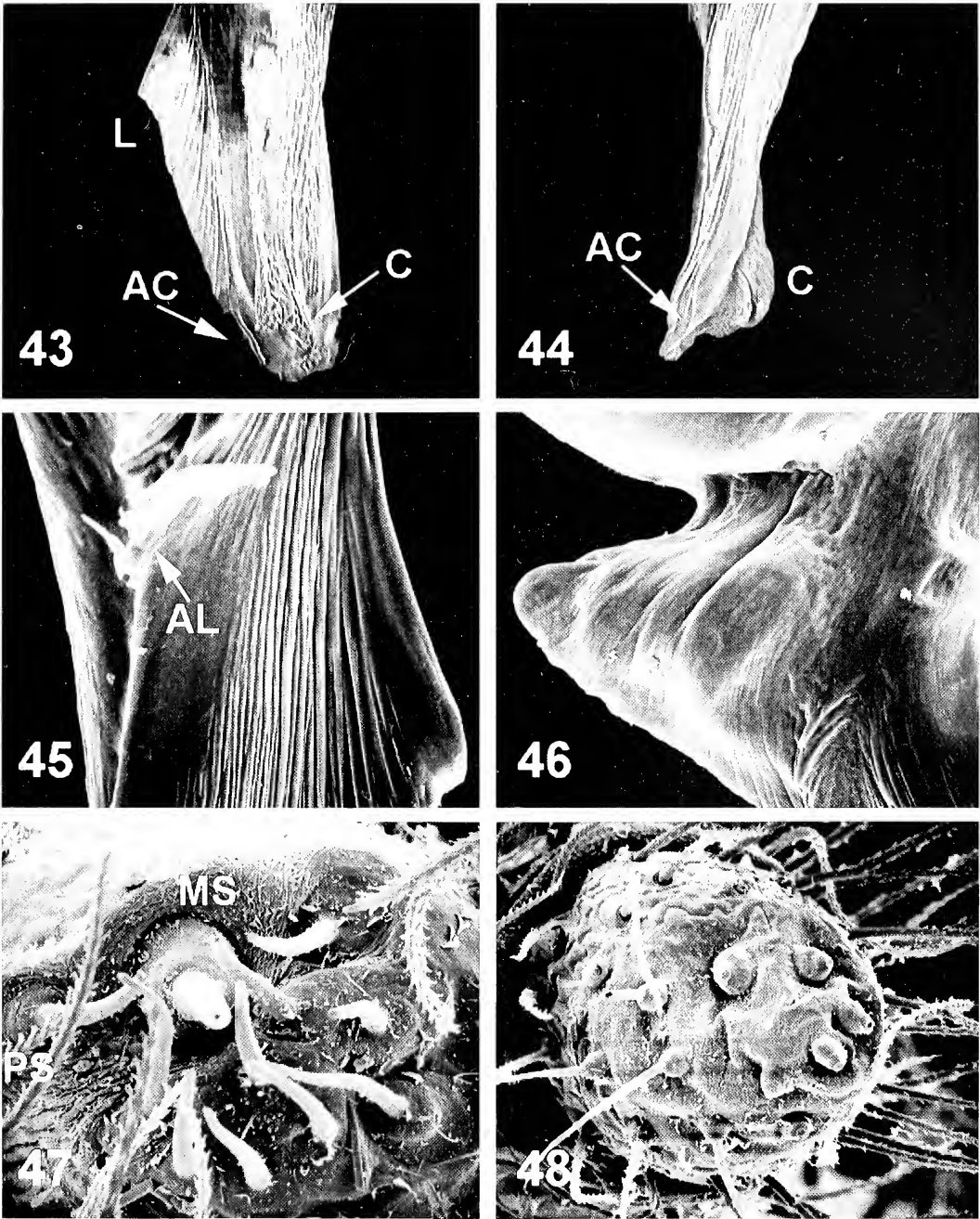
Male bulb (Fig. 39): T slightly smaller than DD; external, internal distal border sloped backwards. DD slightly bent in lateral view, clearly less than 45° ; internal distal border not

expanded. ES more sclerotized than IS; IS truncated at DD middle part. DD tip (Figs. 43–45) straight in lateral view. C present, short; distal end on DD internal tip; well-developed; located close to DD distal tip; proximal border sharply decreasing; distal border stepped, upper tip not projected, pointed; external side hollowed. AC present. LF absent. L well-developed; external border not sclerotized, laterally slightly folded; distal border divergent, continuous. AL present, very poorly developed; proximal border in posterior view toothed. P (Fig. 46) fused to T; perpendicular to T in lateral view; lateral length from $\frac{2}{5}$ – $\frac{1}{2}$ of T width; ridge present, perpendicular to T, not expanded; upper margin slightly toothed, mainly on external side, on its distal part, very few teeth; not distally projected; back margin not folded.

Female: (from Cueva Felipe Reventón, Icod de los Vinos, Tenerife; num. 2744, UL). Figs. 40–42, 47, 48. All characters as in male except: Carapace 2.98 mm long; maximum width 2.37 mm; minimum width 1.44 mm. Brownish-orange, uniformly distributed. AME diameter 0.12 mm; PLE 0.11 mm; PME 0.09 mm; PME about $\frac{3}{5}$ PME diameter from PLE.

Chelicerae 1.3 mm long; fang 1.21 mm. Leg lengths of female described above: fe1 3.45 mm (all measurements in mm); pa1 1.72; ti1 2.33; me1 2.23; ta1 0.51; total 10.24; fe2 2.42; pa2 1.68; ti2 2.19; me2 2.1; ta2 0.56; total 8.95; fe3 1.96; pa3 1.12; ti3 1.44; me3 1.86; ta3 0.51; total 6.89; fe4 2.79; pa4 1.49; ti4 2.33; me4 2.7; ta4 0.6; total 9.91; relative length $1 > 4 > 2 > 3$; palp: fe 1.4; pa 0.6; ti 0.6; ta 0.93; total 3.53. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.0–1.1; distal 1.0–0; ti3 ventral spines arranged in two bands: proximal 2–1.3–0.2–1; distal 1.1–0.1; with two terminal spines. Fe4 dorsal spineless; ti4 dorsal spines arranged in two bands: proximal 0.1–0; distal 1.0–0; ti4 ventral spines arranged in two bands: proximal 1.3–2.0; distal 1.0–0; with two terminal spines.

Abdomen 4.19 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.072–0.09 mm long; medium thickness, curved, compressed, blunt, tip not enlarged; uniformly, thickly distributed. Vulva (Figs. 40–42) arch-like in dorsal view, frontally pointed; as wide as long; DF wide. MF poorly developed. VA frontal region completely sclerotized; posterior re-



Figures 43–48.—*Dysdera brevispina*, right male bulb and female spinnerets. 43, DD frontal; 44, DD external; 45, DD posterior; 46, P external; 47, Right ALS; 48, Right PLS.

gion sclerotized at anterior area; small scale on back border internal part. AVD hardly visible. S attachment not projected under VA; arms as long as DA, straight; tips dorsally projected; neck as wide as arms. TB usual shape. ALS (Figs. 47, 48) with PS; remaining piri-

form spigots more external than MS, arranged in three rows; 9 + 1 piriform gland spigots; PMS, PLS with 10–15 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 2.37–3.63 mm,

Table 4.—Intraspecific spination variability of *Dysdera chioensis*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia palp dorsal	0	1.0.0	0	0
Tibia 3 dorsal	0-1.0-2.0-1	0-1.0-2.0-1	0.0-1.0	1.0-1.1
Tibia 4 dorsal	0.0-2.0-1	1.0-3.1	0	1.0-2.1
Tibia 1 ventral	0.0-1.0	0.0-2.0	0	0
Tibia 2 ventral	0	0.1-2.0	0	0
Tibia 3 ventral	0.0-2.0-1	1.2.0-1	0	1.0-1.0-1
Tibia 4 ventral	0-1.2.0-1	0-1.1-2.1	0-1.0-2.0	0-1.0-1.1
Number of spines				
Patella palp dorsal			1-2	
Patella 3 ventral			0-3	
Patella 4 ventral			0-2	
Number of rows		Number of spines		
Femur 1 frontal	1		1-2	
Femur 2 frontal	1		2-3	
Femur 3 dorsal	2		2-5/1-2	
Femur 4 dorsal	2		1-2/5-9	

female from 2.84–3.47 mm. Carapace frontal lateral borders parallel. Specimens from caves may show certain reduction in eye size. PLE-PME from $\frac{1}{3}$ – $\frac{3}{5}$ diameter, AME separation from $\frac{3}{5}$ –1 diameter apart. Occasionally, D as large as B. In general, cheliceral teeth are small; S arms slightly curved. Spination variability in Table 3.

Additional material examined.—**TENERIFE:** *Icod de los Vinos:* Cueva Felipe Reventón, ? May 1994, 1 ♀ (M. Arechavaleta, num. 2798 UL); ? May 1994, 1 ♀ (M. Arechavaleta, num. 2806 UL). *Cueva del Viento-Sobrado,* 14 April 1983, 1 ♀ (J.L. Martín, num. 2521 UL). *Santa Cruz de Tenerife:* El Bailadero, 27 November 1993, 1 ♀ (M.A. Arnedo & C. Ribera, num. 2588 UB). *Santa Ursula:* Bco. del Pino, (8411 T/C -T), 21–28 July 1985, 1 ♀ (J.M. Peraza, num. 2616 MCNT).

Distribution.—Tenerifean endemic. Known from several localities spread through the island’s northern slopes (including Anaga). One single locality on south-western slopes (Vilafior), collected in MSS trap. Unknown from Teno massif.

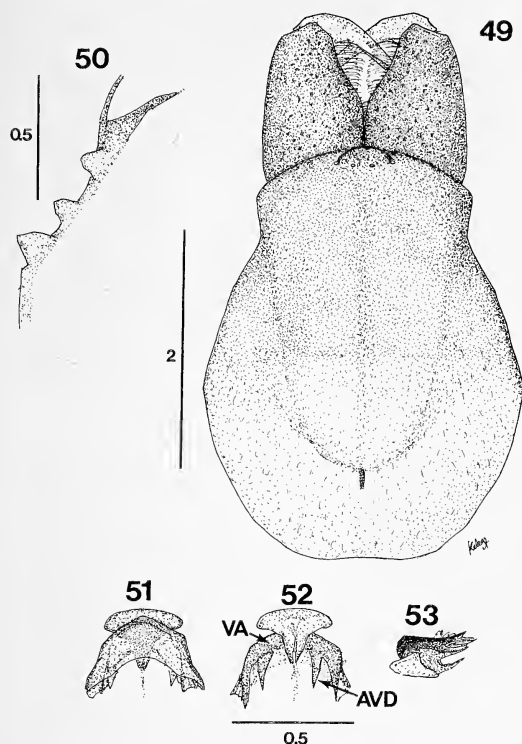
Comments.—After examination of the *D. moquinalensis* holotype, no distinctive morphological difference from *D. brevispina*, apart from the highly polymorphic carapace color, could be found. The only difference of *D. vilaflorensis* holotype from *D. brevispina* is an overall smaller size.

Dysdera chioensis Wunderlich 1991
Figs. 49–53, 73, 74, Table 4

Dysdera chioensis Wunderlich 1991: 291, figs. 21–23 [♀]. Holotype female from Cueva Grande del Chío, Guía de Isora, Tenerife, Canary Islands; 29 June 1985, G.I.E.T. leg.; num. T-GC-5; Stored at UL. Examined. –Wunderlich 1991: 284–287.

Diagnosis.—*Dysdera chioensis* can be distinguished from all other *Dysdera* species, except *D. labradaensis*, by distinct reduction of eye size and presence of spines on frontal legs. Its smaller size and spinated pedipalps distinguish this species from *D. labradaensis*. It differs from the morphologically similar species *D. guayota* new species by having remarkably reduced eyes and presence of spines on palps, and in females by presence of tooth-like expansions in vulva ventral arch (VA) (Figs. 52, 53).

Description.—*Holotype female:* Figs. 49–53, 73–74. Carapace (Fig. 49) 3.73 mm long; maximum width 3.03 mm; minimum width 2 mm. Reddish-orange, frontally darker, becoming lighter towards back; smooth with some black granular material mainly at front; hairy, covered with black hairs mainly at lateral and back borders. Frontal border roughly round, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders slightly convergent; sharpened at maximum dorsal width point, back lateral bor-



Figures 49–53.—*Dysdera chioensis*. 49, Carapace, dorsal; 50, Left chelicera, ventral; 51, Vulva, dorsal; 52 Vulva, ventral; 53, Vulva, lateral. Scale bars in mm.

ders rounded; back margin wide, slightly bilobed. Eyes markedly reduced in size. AME diameter 0.09 mm; PLE 0.05 mm; PME 0.03 mm; AME separation 1.02 mm; AME-PLE separation 0.05 mm; PLE-PME separation 0.14 mm; PME separation 0.16 mm. Labium trapezoid-shaped, base wider than distal part; longer than wide at base; semicircular groove at tip. Sternum yellowish-orange, darkened on borders; smooth; uniformly covered in slender black hairs.

Chelicerae (Fig. 50) 1.77 mm long, about $\frac{1}{3}$ of carapace length in dorsal view; fang medium-sized, 1.16 mm; basal segment dorsal side completely covered with piligerous granulations (distally scarce), ventral side smooth. Chelicera inner groove short, about $\frac{1}{3}$ cheliceral length; armed with three teeth and lamina at base; $B > D = M$; D round, located roughly at center of groove; B close to basal lamina; M close to B. Legs yellow. Lengths of female described above: fe1 2.7 mm (all measurements in mm); pa1 1.68; ti1 2.14; me1 1.91; ta1 0.6; total 9.03; fe2 2.37; pa2 1.63; ti2 2.07;

me2 1.96; ta2 0.6; total 8.63; fe3 2.16; pa3 1.21; ti3 1.68; me3 2.1; ta3 0.65; total 7.8; fe4 2.56; pa4 1.4; ti4 2.1; me4 2.51; ta4 0.65; total 9.22; relative length $4 > 1 > 2 > 3$; palp: fe 1.9; pa 0.74; ti 0.65; ta 0.93; total 4.22. Spination: Palp pa 1, palp ti 1 medial internal. Fe1 1 distal, anterior margin. Fe2: 3-2 distal, anterior margin. Fe3 dorsal spines in two rows: anterior 5; posterior 1 (distal); pa3 spineless; ti3 dorsal spines arranged in two bands: proximal 1.2.1; distal 1.0.1.; ti3 ventral spines arranged in two bands: medial-proximal 1.2.1; distal 1.0.0-1; with two terminal spines. Fe4 dorsal spines in two rows: anterior 1; posterior 7-5; pa4 1 ventral medial; ti4 dorsal spines arranged in three bands: proximal 0.0.0-1; medial-proximal 1.1.1; distal 1.0.1; ti4 ventral spines arranged in three bands: proximal 0.2.0; medial-proximal 1.1.1; medial-distal 0; distal 1.1.1; with two terminal spines. Dorsal side of frontal legs, ventral side of palps covered with hairs, lacking a granular surface. Claws with 10–14 teeth; hardly larger than claw width.

Abdomen 5.12 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.216–0.234 mm long; thin, curved, compressed, pointed; uniformly, thickly distributed. Vulva (Figs. 51–53) arch-like in dorsal view, frontally pointed; slightly wider than long; DF wide. MF well-developed. VA frontal region completely sclerotized; posterior region sclerotized at anterior area; tooth-shaped expansion from internal back border; not joined to lateral sclerotization, slightly shorter than DA lateral margins. AVD clearly recognizable. S attachment projected under VA; arms are shorter than DA, straight; tips not projected; neck as wide as arms. TB usual shape. ALS (Figs. 73, 74) with PS; remaining piriform spigots more external than MS, arranged in two rows; 9 + 1 piriform gland spigots; PMS, PLS with 5–10 aciniform gland spigots.

Male: Unknown.

Intraspecific variation.—Female cephalothorax ranges in length from 3.36–5.6 mm. D at center of chelicera groove or at tip. Specimens from Los Roques, S arms longer. Spination variability in Table 4.

Additional material examined.—**TENERIFE:** *Guía de Isora*: Cueva Grande del Chío, 28 January 1993, 1 juv. (P. Oromí, num. 2545 UL); 21 October 1994, 1 ♀ (Arnedo & Ribera, num. 4821 (T32) UB).

Table 5.—Intraspecific spination variability of *Dysdera cribellata*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.0.1	0-1.0.0	0	1.0.0
Tibia 4 dorsal	1.0.1	0	0	0-1.0.0-1
Tibia 3 ventral	0-1.0-1.0	0	0	0-1.0.0
Tibia 4 ventral	0-1.1.0	0-1.0-1.0	0	0-1.0.0
	Number of rows		Number of spines	
Femur 3 dorsal	0		0	
Femur 4 dorsal	0		0	

La Orotava: Cueva de Los Roques, 11 August 1986, 1juv. (J.L. Martín, num. 2536 UL); November 1995, 1♀ (P. Oromí, num. 2965 UB); 27 October 1991, 1♀ (C. Ribera, num. 2566 UB); November 1995, 1♀ (P. Oromí, num. 2967 UB).

Distribution.—Tenerifean endemic. Known from two lava tubes located on dry, south-western slopes.

Comments.—Even though several new female specimens have been collected and a new locality has been found for this species, the male remains unknown.

Dysdera cribellata Simon 1883
Figs. 54–65, Table 5

Dysdera cribellata Simon 1883 (nec. Simon 1907: 258–259, fig. 257 [♂]; incorrect identification): 294–295, fig. 17 [♂]. Type male lost. Type female from Canary Islands, unknown locality; unknown data, M. Verneau leg.; num. B-536; Stored at MNHN. Examined. -Bösenberg 1895: 7. -Reimoser 1919. -Denis 1941: 108. -Schmidt 1973: 360–361. -Arnedo et al. 1996: 243.

D. medinae Wunderlich 1991: 299, figs. 57–60 [♂, ♀]. Holotype ♂ and paratype ♀ from Monte de las Mercedes, La Laguna, Tenerife, Canary Islands; in II, M. Knösel leg.; Stored at SMF. Holotype not examined, paratypes examined. New synonymy.

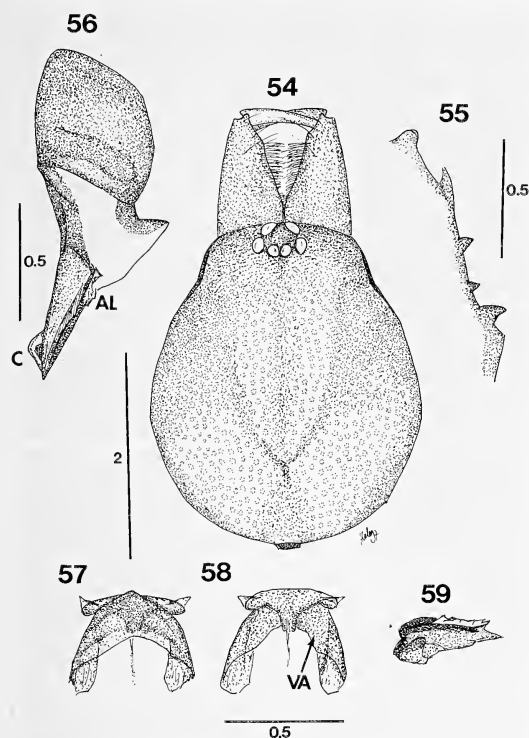
D. volcania Ribera, Ferrández & Blasco 1985: 59–61, figs. 3E-F [♀] (♀, non♂). Paratype female (allotype) from Cueva de Felipe Reventón, Icod de los Vinos, Tenerife, Canary Islands; 3 March 1984, P. Oromí leg.; num. T-FR-107. Stored at UL. Examined. Incorrect identification.

Diagnosis.—*Dysdera cribellata* can be distinguished from all other Canarian species by its markedly foveate carapace, cheliceral basal tooth (B) being the largest (Fig. 55) and a lack of cheliceral granulation. It can be distinguished from the similar *D. insulana* by its

foveate carapace and distinctive spination pattern (Table 5).

Description.—*Male*: (from Sima de la Robada, Santa Cruz de Tenerife, Tenerife; num. 2552, UL). Figs. 54–56, 60–63. Carapace (Fig. 54) 3.22 mm long; maximum width 2.75 mm; minimum width 1.77 mm. Dark red, darkened at borders; heavily foveate, covered with circular depressions, some black granular material mainly at front. Frontal border roughly round, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders slightly divergent; rounded at maximum dorsal width point, back lateral borders rounded; back margin wide, straight. AME diameter 0.23 mm; PLE 0.21 mm; PME 0.16 mm; AME on edge of frontal border, separated one from another about $\frac{2}{5}$ of diameter, close to PLE; PME very close to each other, about $\frac{1}{3}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base; semicircular groove at tip. Sternum dark red, darkened on borders; heavily wrinkled; covered in hairs mainly on margin.

Chelicerae (Fig. 55) 1.35 mm long, about $\frac{1}{3}$ of carapace length in dorsal view; fang medium-sized, 1.16 mm; basal segment smooth, with no granulations. Chelicera inner groove long, about $\frac{1}{2}$ cheliceral length; armed with three teeth and lamina at base; $B > D > M$ (not very different, small); D trapezoid, located roughly at center of groove; B close to basal lamina; M close to B. Legs orange. Lengths of male described above: fe1 2.79 mm (all measurements in mm); pa1 1.86; ti1 2.61; me1 2.51; ta1 0.56; total 10.33; fe2 2.51; pa2 1.63; ti2 2.33; me2 2.28; ta2 0.56; total 9.75; fe3 2; pa3 1.12; ti3 1.49; me3 1.86; ta3 0.51; total 6.98; fe4 2.75; pa4 1.49; ti4 2.33; me4 2.7;



Figures 54–59.—*Dysdera cribellata*. 54, Carapace, dorsal; 55, Right chelicera, ventral; 56, Left male bulb, external; 57, Vulva, dorsal; 58, Vulva, ventral; 59, Vulva, lateral. Scale bars in mm.

ta4 0.6; total 9.87; relative length: $1 > 4 > 2 > 3$; palp: fe 1.4; pa 0.7; ti 0.7. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in three bands: proximal 1.0.1; medial-proximal 0–1.0.0; distal 1.0.0; ti3 ventral spines arranged in two bands: proximal 1.1.1; distal 1.0.0; with two terminal spines. Fe4 dorsal spineless; ti4 dorsal spines arranged in two bands: proximal 1.0.1; distal 0.0.1; ti4 ventral spines arranged in two bands: proximal 1.1.0; distal 1.0.0; with two terminal spines. Dorsal side of frontal legs smooth; ventral side of palp covered with hairs, lacking a granular surface. Claws with 10–14 teeth, length twice claw width.

Abdomen 3.68 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.045–0.054 mm long; thin, curved, compressed, pointed; uniformly, thickly distributed.

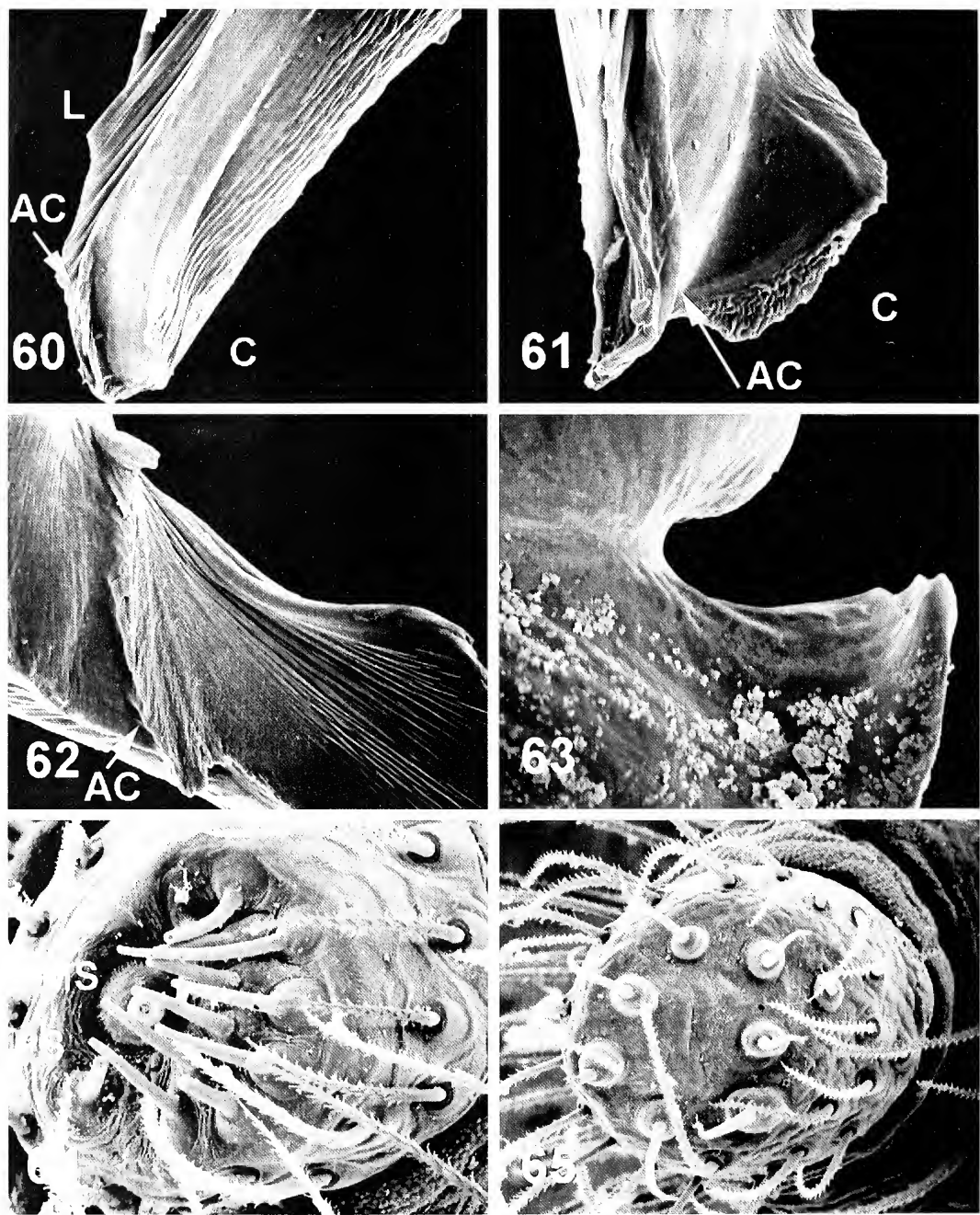
Male bulb (Fig. 56): T slightly smaller than DD; external, internal distal border sloped backwards. DD slightly bent in lateral view, clearly less than 45° ; internal distal border not expanded. ES more sclerotized than IS; IS

truncated at DD middle part. DD tip (Figs. 60–62) straight in lateral view. C present, short; distal end on DD internal tip; well-developed; located close to DD distal tip; proximal border sharply decreasing; distal border stepped, upper tip not projected, sloped; external side hollowed. AC present. LF absent. L well-developed; external border not sclerotized, laterally slightly folded; distal border divergent, not continuous; upper sheet strongly folded at middle. AL present, very poorly developed; proximal border in posterior view toothed. P (Fig. 63) fused to T; perpendicular to T in lateral view; lateral length from $\frac{2}{5}$ – $\frac{1}{2}$ of T width; ridge present, perpendicular to T, not expanded; upper margin slightly toothed, mainly on external side, on its distal part, few teeth; not distally projected; back margin slightly folded towards internal side.

Lectotype female: Figs. 57–59, 64, 65. Carapace 3.82 mm long; maximum width 3.08 mm; minimum width 1.82 mm. Brownish-orange. Anterior lateral borders parallel; rounded at maximum dorsal width point, back lateral borders straight. AME diameter 0.23 mm; PLE 0.21 mm; PME 0.16 mm; AME separated one from another about $\frac{2}{3}$ of diameter; PME about $\frac{2}{5}$ diameter from PLE. Sternum orange, uniformly distributed; wrinkled.

Chelicerae 1.67 mm long; fang 1.3 mm. Legs yellow. Lengths of female described above: fe1 2.98 mm (all measurements in mm); pa1 2.05; ti1 2.52; me1 2.47; ta1 0.56; total 10.58; fe2 2.66; pa2 1.86; ti2 2.33; me2 2.28; ta2 0.56; total 9.69; fe3 2.28; pa3 1.3; ti3 1.54; me3 1.91; ta3 0.56; total 7.59; fe4 3.03; pa4 1.63; ti4 2.33; me4 2.84; ta4 0.65; total 10.48; relative length $1 > 4 > 2 > 3$; palp: fe 1.49; pa 0.83; ti 0.74; ta 0.93; total 3.99. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.0.1; distal 1.0.0; ti3 ventral spines arranged in two bands: proximal 0.1.0; distal 1.0.0; with two terminal spines. Fe4 dorsal spineless; ti4 dorsal spines arranged in one band: proximal 1.0.1; ti4 ventral spines arranged in two bands: proximal 1.1.0; distal 1.0.0; with two terminal spines.

Abdomen 4.84 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.054 mm long; thin, curved, compressed, pointed; uniformly, thickly distributed. Vulva (Figs. 57–59) arch-like in dorsal view, frontally pointed; slightly



Figures 60–65.—*Dysdera cribellata*, right male bulb and female spinnerets. 60, DD frontal; 61, DD external; 62, DD posterior; 63, P external; 64, Right ALS; 65, Right PLS.

wider than long; DF wide. MF poorly developed. VA frontal region completely sclerotized; posterior region sclerotized at anterior area. AVD hardly visible. S attachment not projected under VA; arms are slightly shorter than DA, straight; tips not projected; neck as

wide as arms. TB usual shape. ALS (Figs. 64, 65) with PS; remaining piriform spigots more external than MS, arranged in two rows; 11 + 1 piriform gland spigots; PMS, PLS with 5–10 aciniform gland spigots.

Intraspecific variation.—Male cephalo-

thorax ranges in length from 3.62–4.66 mm, female from 3.82–3.96 mm. Carapace frontal lateral margins usually parallel. AME separation from $\frac{2}{5}$ – $\frac{3}{5}$ diameter. PLE–PME from $\frac{1}{4}$ – $\frac{1}{2}$ diameter. Sternum ornamentation somewhat reduced. Spination variability in Table 5.

Additional material examined.—**TENERIFE:** ?; 21 December 1940, 1 ♀ (J. Denis, num. BMNH 1940.12.21.15 BMNH). *La Laguna:* El Moquinal, 28 November 1993, 1 ♀ (Arnedo & Ribera, num. 4794 (T29) UB); 28 November 1993, 1 ♀ (Arnedo & Ribera, num. 4817 (T20) UB). *Santa Cruz de Tenerife:* Cruz del Carmen, 12 May 1996, 2 ♂ (M. Naranjo, num. 3148 UB); 12 May 1996, 1 ♀ (M. Naranjo, num. 3149 UB); 12 May 1996, 1 ♂ (M. Naranjo, num. 3150 UB); 12 May 1996, 1 ♀ (M. Naranjo, num. 3151 UB). Monte de las Mercedes, 24 May 1996, 1 ♂ (P. Oromí, num. 3162 UB); 24 May 1996, 1 ♂ (P. Oromí, num. 3163 UB). Sima de la Robada, 13 February 1992, 1 ♀ (P. Oromí, num. 2514 UL). Taganana, 20 February 1989, 1 ♀ (García Alayón, num. 2599 UL). *Dysdera medinae:* **TENERIFE:** *Santa Cruz de Tenerife:* Monte Aguirre, 4 June 1986, 1 ♂ paratype (C.G. Campos, num. 2741 UL).

Distribution.—Tenerifean endemic. Known from several localities spread through the northern slope of the island, including the Anaga and Teno massifs.

Comments.—The original male material of this species seems to have been lost. However, the female used in the original description was available for the present study.

The original description of *D. cribellata* (Simon 1883), as well as the remaining *Dysdera* species described in that work, lacked any reference to the locality. In a subsequent paper (Simon 1907) the original locations were assigned using new labelled material. Thus, *D. cribellata* was thought to be present in La Palma. However, after examination of the drawings of the male bulb drawings from both the description and the redescription, they were actually considered to belong to different species (Arnedo et al. 1996). Therefore, the report of this species in La Palma was due to a incorrect identification. The presence of *D. cribellata* in Tenerife has been documented previously (Bösenberg 1895; Denis 1941).

Examination of the *D. medinae* male paratype and the *D. volcania* female allotype did not show any diagnostic character with regard to *D. cribellata*. In both cases misidentifica-

tion was probably due to unavailability of *D. cribellata* type specimens.

Dysdera crocota C.L. Koch 1839

Dysdera crocota C.L. Koch 1839: 81. -Schmidt 1973: 360–361. -Wunderlich 1991: 284–286, 292–293, figs. 28–31 [♂, ♀]. -Arnedo et al. 1996: 252–253. -Arnedo & Ribera 1997.

Dysdera inaequiscapillata Wunderlich 1991: 295, figs. 42–46 [♂, ♀]. Holotype male from Punta Hidalgo, La Laguna, Tenerife, Canary Islands; 14 February 1986, R. Wiss leg.; num. 3934; Stored at UL. Examined. New synonymy.

Diagnosis.—*Dysdera crocota* can be distinguished from all other Canarian species, except *D. lancerotensis* Simon 1907, by carapace with a bilobed posterior margin in both sexes, in males by having bulb posterior apophysis (P) not fused to tegulum (T) and a strongly sclerotized apophysis in frontal-distal tip of distal division (DD), and in females by an unsclerotized frontal part of vulva ventral arch (VA). Males and females differ from *D. lancerotensis* by lack of spines on frontal legs (although not always so), males by shape of the bulb frontal distal division tip and posterior apophysis with only two ridges, and females by rectangular shape of vulva dorsal arch (DA) (in dorsal view) and projection of ventral under dorsal arch (in dorsal view).

Material examined.—**TENERIFE:** ?; 18/4/84, 1 ♂ 2 ♀ (N.P. Ashmole, num. 2715 UL). *Adeje:* Playa Paraiso, 10–50 m, 24–30 December 1994, 1 ♀ (F. Gasparo, FG). *Buenavista:* Teno Alto, ? March 1994, 1 ♀ (Oromí, num. 2937 UB); 1 juv., (Oromí, num. 4814 (T6) UB); 1 ♂, (Oromí, num. 4819 (T2) UB); 3 ♀ (P. Oromí, num. 4823–5 UB). *El Rosario:* Tabaiba, MSS-1, 9 October 1990, 1 ♀ (A.L. Medina, num. 2774 UL). *El Sauzal:* Around Cueva Labrada, ? November 1993, 5 ♀ (Arnedo & Ribera, num. 4807–11 UB); 1 ♂ (Arnedo & Ribera, num. 4832 (T46) UB); 1 juv. (Arnedo & Ribera, num. 4834 (T49) UB). *El Tanque:* El Tanque, 550m, 26 December 1994, 1 ♀ (F. Gasparo, FG). *Icod de los Vinos:* Altos de El Sobrado, 15 March 1995, 1 ♂, (G. Ortega, MCNT). Icod, 21 December 1982, 1 ♀ (P. Morales, num. 2768 UL). *Garachico:* La Montañeta, 18 February 1996, 8 ♂ 4 ♀ 3 juv. (Arnedo & Oromí, num. 3106–17 UB). *La Laguna:* Co-comoto, ? February 1989, 1 ♀ (C. Deniz, num. 2596 UL). El Moquinal, 28 November 1993, 1 ♀ (Arnedo & Ribera, num. 4812 (T5) UB); 23 January 1997, 1 ♀ (P. Oromí, num. 3197 UB). La Laguna, 12 February 1987, 1 ♂ (C.G. Campos, num. 2739 at UL); 28 December 1987, 1 ♂ (C.G. Campos, num. 2688 UL); ? November 1988, 1 juv. (C. Deniz, num. 2597

UL). Las Mercedes, 24 November 1982, 1♂ (A. Santaella, num. 2777 UL); 25 October 1984, 1♂ (C.G. Campos, num. 2740 UL). Los Rodeos, 1♂, 3♀ (R.G. Becerra, num. 2582 RG). Mesa Mota, 4 June 1983, 1♀ (R. Vonk, num. 2773 UL). San Diego, 24 November 1982, 1♀ (E. Caverio, num. 2767 UL). *La Matanza de Acentejo*: La Matanza, 900 m, 2 June 1996, 1♀ (M. Naranjo, num. 3172 UB); 1♂, 1♀, 4juv., (M. Naranjo, 3187 UB). *La Ortava*: Around Cueva del Bucio, 21 October 1994, 1♂ (Arnedo, Ribera & Serra, num. 4003 UB). Agumansa, La Caldera, 21 October 1994, 2♂, 1♀ (Arnedo, Ribera & Serra, num. 4004-6 UB). *La Victoria de Acentejo*: Las Lagunetas, 4 February 1989, 1♀ (O. Torres, num. 2690 UL); 30 October 1994, 1♀ (P. Oromí, num. 4002 UB); 25 April 1995, 1♀ (P. Oromí, num. 3182 at UB), 1 May 1995, 1♀ (Oromí, num. 4175 (134) UB). *Los Realejos*: Los Realejos, 25 February 1983, 1♀ (A. Fox, num. 2769 UL). *Los Silos*: Erjos, 15 April 1973, 1♀ (J.M. Fernández, num. 2503a UB). *Santa Cruz de Tenerife*: Cruz del Carmen, 12 May 1996, 1juv. (M. Naranjo, num. 3144 UB); 25 January 1997, 1♀ (P. Oromí, num. 3193 UB). Parque de Anaga, 6 February 1988, 1♀ (P. Suárez, num. 2689 UB). *Santa Ursula*: Monte de Santa Ursula, 13 December 1996, 1♀, (P. Oromí, num. 3211 UB). *Santiago del Teide*: Los Gigantes, 28 March 1994, 1♂ (P. Oromí, num. 2816 UB). *D. inaequuscapillata*: **TENERIFE**: *La Laguna*: Punta Hidalgo, 14 December 1986, 1 paratype, (R. Wiss, num. 2623 SMF); 14 December 1986, 1juv. (R. Wiss, num. 2731 UL); 23 December 1986, 1♀ (C.G. Campos, num. 2729 UL); 23 December 1986, 2♂ (C.G. Campos, num. 2738 UL). Las Mercedes, ? June 1984, 1♂, (S. Morales, num. 2730 UL).

Distribution.—Cosmopolitan species, spread all over the world, probably due to human introduction.

Comments.—The presence of *D. crocota* has been documented in all the islands of the archipelago, with the exception of Fuerteventura and Lanzarote. In the Canaries, *D. crocota* is always found in habitats disturbed by human activities. It may suggest that this species has recently been introduced in the archipelago by man.

After examination of several types of *D. inaequuscapillata* Wunderlich 1991, they were considered to belong to *D. crocota*. This misidentification is extraordinarily surprising. The original author was aware of the presence of *D. crocota* in the Canaries and even, in the same work, mentioned and drew several characters of *D. crocota*. However, he described *D. inaequuscapillata* as a different species on

the basis of the 'uniqueness' of its male bulb in the Canaries.

Dysdera curvisetae Wunderlich 1987

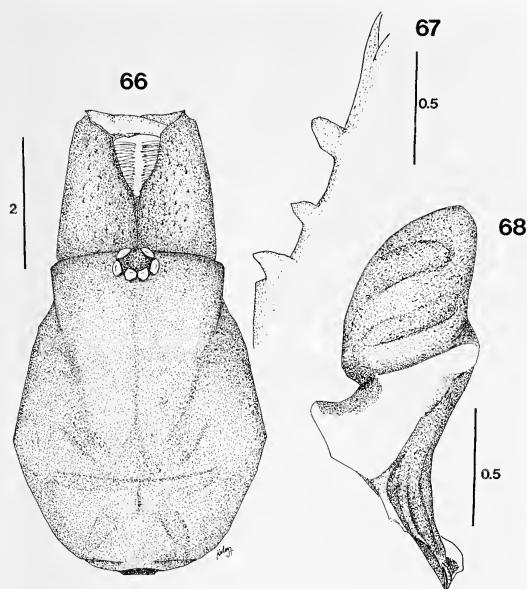
Figs. 66–72

Dysdera curvisetae Wunderlich 1987: 291, figs. 12–17 [♂]. Holotype male from small cave at the North coast of San Marcos, Icod de los Vinos, Tenerife, Canary Islands; in VIII, J. Wunderlich leg.; Stored at SMF. Examined. —Wunderlich 1991: 284–287.

Diagnosis.—*Dysdera curvisetae* can be distinguished from all other *Dysdera* species, except *D. ratonensis* and *D. verneui* Simon 1883, by its wide frontal border and diamond-shaped carapace (Fig. 66). It differs from *D. ratonensis* and *D. verneui* by its poorly-spined legs and shape and size of male abdominal dorsal hairs.

Description.—*Holotype male*: Figs. 66–72. Carapace (Fig. 66) 5.42 mm long; maximum width 4.2 mm; minimum width 2.94 mm. Dark red, frontally darker, becoming lighter towards back; slightly foveate at borders, slightly wrinkled with small black fine-textured granular material mainly at front. Frontal border roughly straight, about $\frac{3}{5}$ carapace length; anterior lateral borders convergent; sharpened at maximum dorsal width point, back lateral borders straight; back margin wide, straight; transversal suture on dorsal medial posterior surface. AME diameter 0.32 mm; PLE 0.27 mm; PME 0.23 mm; AME on edge of frontal border, separated one from another about $\frac{2}{3}$ of diameter, close to PLE; PME very close to each other, less than $\frac{1}{4}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base; semicircular groove at tip. Sternum dark red, darkened on borders; very slightly wrinkled, mainly between legs and frontal border; uniformly covered in slender black hairs.

Chelicerae (Fig. 67) 3.08 mm long, about $\frac{2}{5}$ of carapace length in dorsal view; fang long, 2.1 mm; basal segment dorsal, ventral side completely covered with piligerous granulations (small, dense). Chelicera inner groove medium-size, about $\frac{2}{5}$ cheliceral length; armed with three teeth and lamina at base; $D > B > M$ (D, B very similar, all large); D trapezoid, located roughly at center of groove; B close to basal lamina; M at middle of B and D. Legs dark orange-colored. Lengths of male



Figures 66–68.—*Dysdera curvisetae*. 66, Carapace, dorsal; 67, Left chelicera, ventral; 68, Right male bulb, external. Scale bars in mm.

described above: fe1 5.6 mm (all measurements in mm); pa1 3.64; ti1 5.6; me1 5.6; ta1 0.91; total 21.35; fe2 4.41; pa2 3.01; ti2 4.48; me2 2.68; ta2 0.84; total 15.42; fe3 3.64; pa3 1.75; ti3 2.94; me3 3.78; ta3 0.84; total 12.95; fe4 4.4; pa4 2.52; ti4 4.13; me4 5.25; ta4 0.98; total 17.28; relative length: $1 > 4 > 2 > 3$; palp: fe 2.8; pa 1.54; ti 1.47; ta 1.26; total 7.07. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.0.1; distal 1-0.0.0; ti3 ventral spines arranged in two bands: proximal 0-1.1.0; distal 1.0.0; with two terminal spines. Fe4 dorsal spines in two rows: anterior 1; posterior 1; ti4 dorsal spines arranged in three bands: proximal 0.0-1.1; medial-proximal 1.1.1; distal 1.0.0; ti4 ventral spines arranged in three bands: proximal 1.1.0; medial-proximal 0.0-1.0-1; distal 1.0.1; with two terminal spines. Dorsal side of frontal legs, ventral side of palp with a fine-textured, granular, piligerous surface. Claws with 10-14 teeth; hardly larger than claw width.

Abdomen 7.7 mm long; cream-colored; cylindrical. Anterior abdominal dorsal hairs 0.126 mm long (large); medium thickness, curved, compressed, blunt, tip not enlarged; uniformly, thickly distributed. Posterior abdominal dorsal hairs 0.036–0.054 mm long; thick, curved, not compressed, tip enlarged,

distally acuminated; uniformly, thickly distributed. Spinneret gland spigot data not available.

Male bulb (Fig. 68): T slightly smaller than DD; external, internal distal border sloped backwards. DD slightly bent in lateral view, clearly less than 45° ; internal distal border not expanded. IS and ES equally developed; IS truncated at DD middle part. DD tip (Figs. 69–71) straight in lateral view. C present, short; distal end on DD internal tip; well-developed; located close to DD distal tip; proximal border sharply decreasing; distal border stepped, upper tip not projected, pointed; external side hollowed. AC present. LF absent. L well-developed; external border not sclerotized, laterally slightly folded; distal border divergent, most external part perpendicular, continuous. AL present, very poorly developed; proximal border in posterior view fused with DH. P (Fig. 72) fused to T; perpendicular to T in lateral view; lateral length from $\frac{1}{2}$ – $\frac{2}{3}$ of T width; ridge present, perpendicular to T, not expanded; upper margin smooth; not distally projected; back margin not folded.

Female: Unknown.

Intraspecific variation.—Unknown.

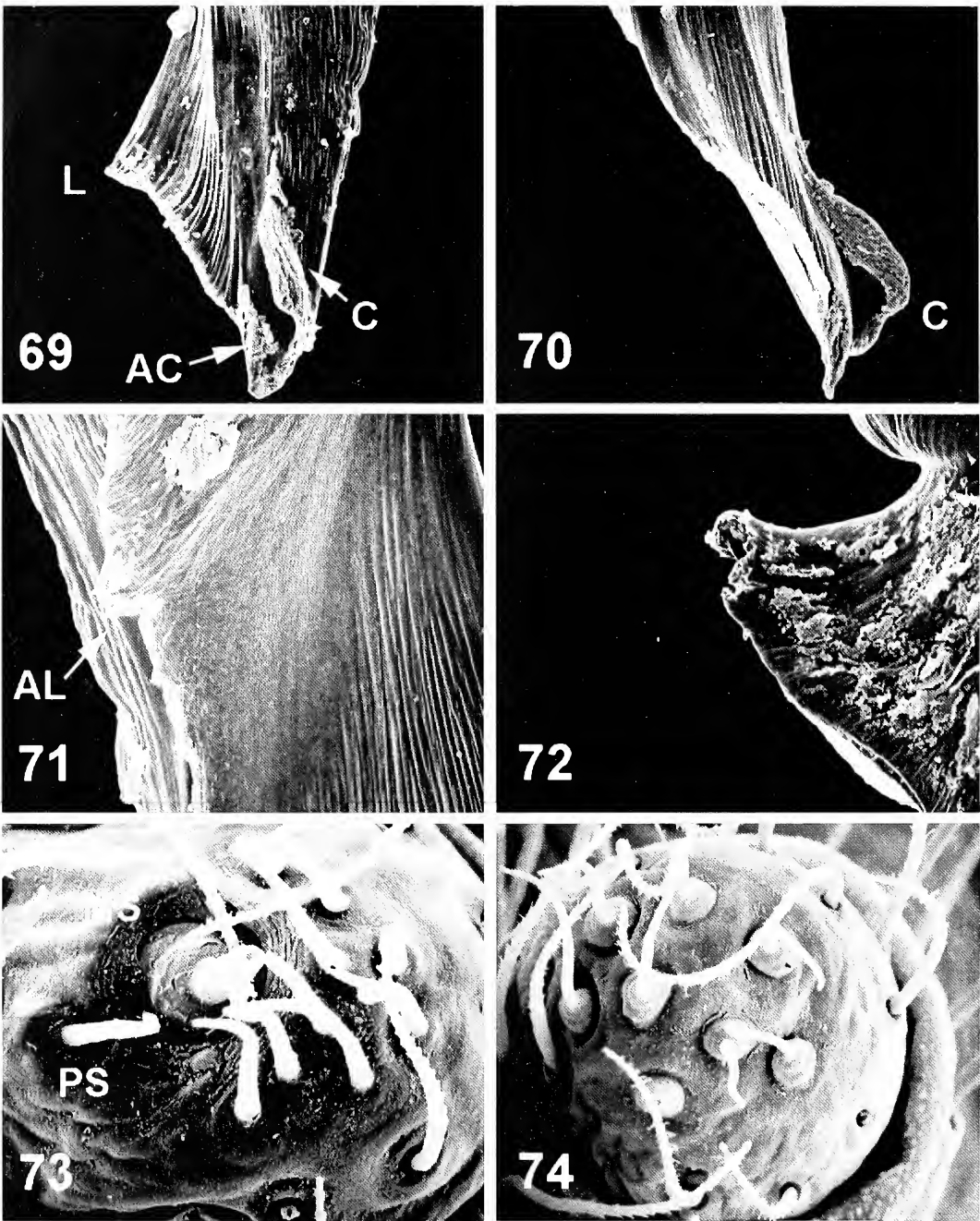
Distribution.—Tenerifean endemic. Known from a single locality on the island's northern slope.

Dysdera esquiveli Ribera & Blasco 1986
Figs. 75–86, Table 6

Dysdera esquiveli Ribera & Blasco 1986: 42–44, fig. 1A–F [δ , φ]. Holotype male and paratype female from Cueva del Viento-Sobrado, Icod de los Vinos, Tenerife, Canary Islands; 23 March 1983, J.L. Martín leg.; δ num. T-CV-118, num. T-CV-119; Stored at UL. Examined. –Wunderlich 1991: 284–287.

Diagnosis.—*Dysdera esquiveli* can be distinguished from all other *Dysdera* species, except *D. hernandezi* new species and *D. gollumi*, by its small size (carapace < 2.5 mm) and complete eye reduction. It differs from *D. gollumi* (male unknown) by its smooth carapace. It differs from the very similar *D. hernandezi* new species (male unknown) by presence of cheliceral granulation, fang shape, and distinct spination pattern (Table 6).

Description.—*Holotype male*: Figs. 75–77, 81–84. Carapace (Fig. 75) 1.96 mm long; maximum width 1.46 mm; minimum width 0.88 mm. Brownish-orange, uniformly distrib-



Figures 69–74.—69–72, *Dysdera curvisetae*, right male bulb. 69, DD frontal; 70, DD external; 71, DD posterior; 72, P external. 73–74, *Dysdera chioensis*, spinnerets. 73, Right ALS; 74, Right PLS.

uted; slightly foveate at borders, wrinkled at middle, covered with tiny granulations. Frontal border roughly round, markedly smaller than $\frac{1}{2}$ carapace length; anterior lateral borders slightly divergent, or parallel; rounded at maximum dorsal width point, back lateral bor-

ders straight; back margin narrow, straight. Eyeless. Labium trapezoid-shaped, base wider than distal part; as long as wide at base (triangle-like); semicircular groove at tip. Sternum orange, uniformly distributed; wrinkled; covered in hairs mainly on margin.

Table 6.—Intraspecific spination variability of *Dysdera esquivei*.

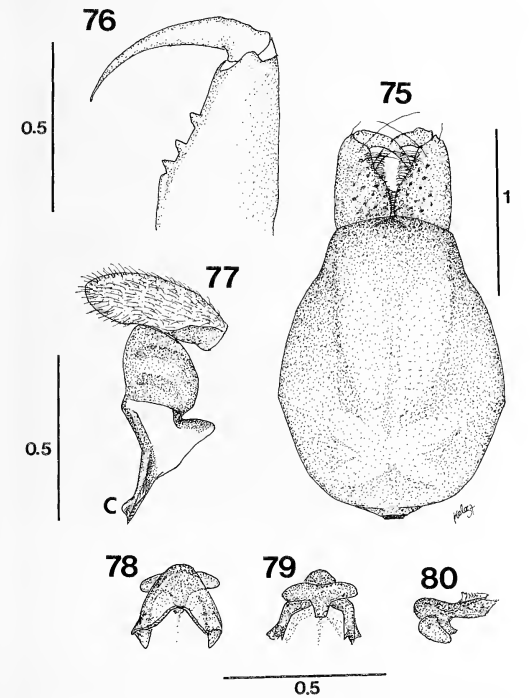
	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.0.0-1	0-1.0-1.0	0	1.0.0-1
Tibia 4 dorsal	0-1.0.0	0-1.0-1.0-1	0	1.0.0-1
Tibia 3 ventral	0-1.0-1.0-1	0	0	0-1.0-1.0
Tibia 4 ventral	0-2.0-1.0	1.1.1	0-1.0-1.0-1	0-1.0.0-1
	Number of rows		Number of spines	
Femur 3 dorsal	1		0-1	
Femur 4 dorsal	2		0-1/1-3	
			Number of spines	
Patella 3 ventral			0-1	
Patella 4 ventral			1-3	

Chelicerae (Fig. 76) 0.67 mm long, about ¼ of carapace length in dorsal view; fang medium-sized, 0.51 mm; basal segment dorsal side completely covered with piligerous granulations (distally scarce), ventral side smooth. Chelicera inner groove medium-size, about ⅔ cheliceral length; armed with three teeth and lamina at base; D = M = B; D triangular, located roughly at center of groove; B close

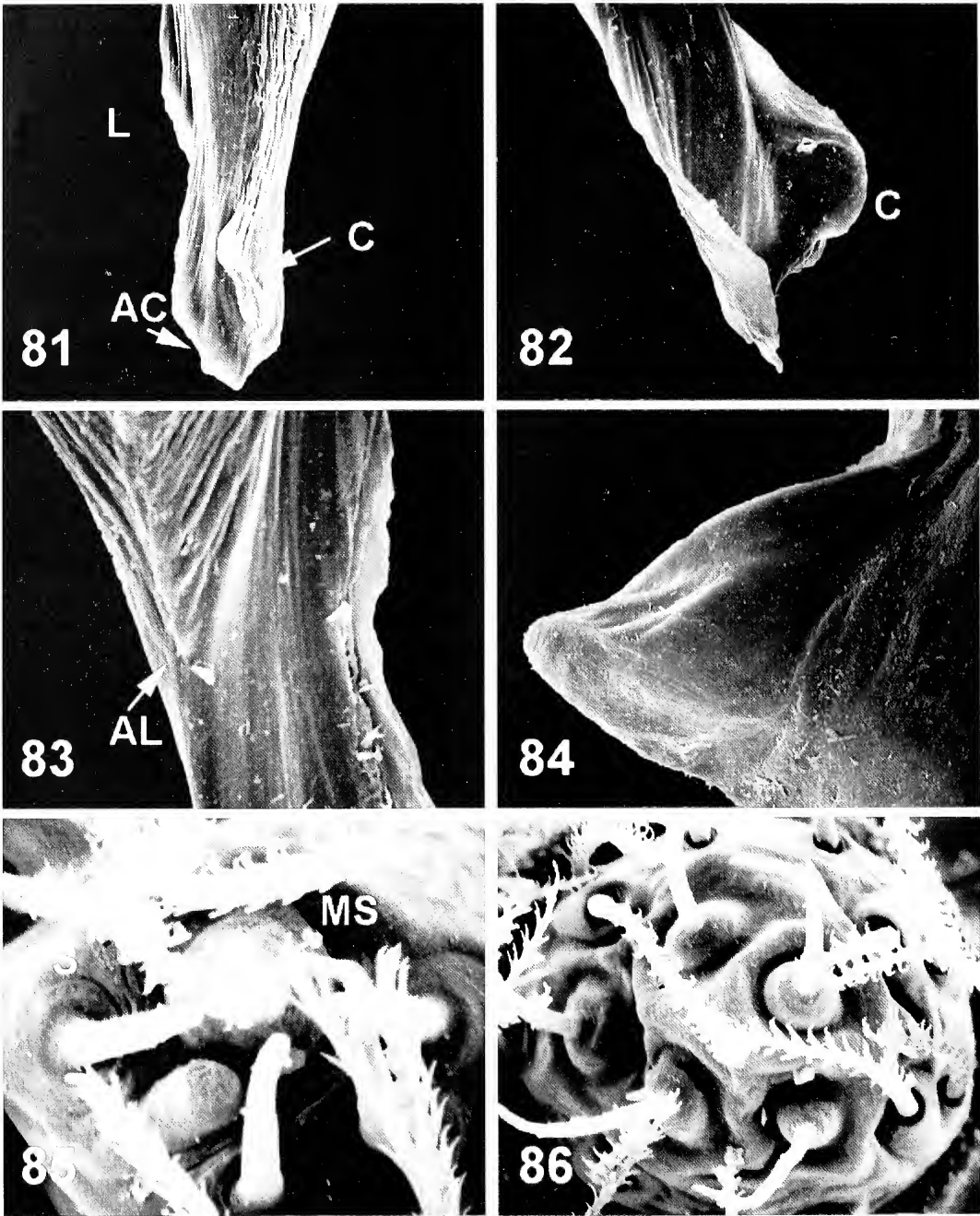
to basal lamina; M close to B. Legs pale yellow. Lengths of male described above: fe1 1.67 mm (all measurements in mm); pa1 1.06; ti1 1.39; me1 1.34; ta1 0.46; total 5.92; fe2 1.52; pa2 0.89; ti2 1.32; me2 1.24; ta2 0.4; total 5.37; fe3 1.11; pa3 0.61; ti3 0.76; me3 1.01; ta3 0.28; total 3.77; fe4 1.52; pa4 0.78; ti4 1.14; me4 1.34; ta4 0.4; total 5.18; relative length: 1 > 2 > 4 > 3; palp: fe 0.86; pa 0.43; ti 0.43; ta 0.51; total 2.23. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; pa3 1-0 ventral; ti3 dorsal spines arranged in two bands: proximal 1.0.0; distal 1.0.0; ti3 ventral spines arranged in two bands: proximal 0.1-0.0; distal 1.0.0; with two terminal spines. Fe4 dorsal spines in one row: 1; pa4 2-3 ventral; ti4 dorsal spines arranged in two bands: medial-proximal 1.0.1; distal 1.0.1; ti4 ventral spines arranged in four bands: proximal 1.0.0; medial-proximal 1.1.1; medial-distal 1.0-1.1; distal 1.0.1; without terminal spines. Dorsal side of frontal legs smooth; ventral side of palp smooth; long, spine-like hairs on ventral posterior ti, fe. Claws with 10–14 teeth, length twice claw width.

Abdomen 2.28 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.027 mm long; medium thickness, roughly straight, not compressed, blunt, tip enlarged; uniformly, scanty distributed.

Male bulb (Fig. 77): T slightly smaller than DD; external distal border straight; internal sloped backwards. DD slightly bent in lateral view, clearly less than 45°; internal distal border not expanded. IS and ES equally developed; IS truncated at DD middle part. DD tip straight in lateral view. C present, short; distal



Figures 75–80.—*Dysdera esquivei*. 75, Carapace, dorsal; 76, Left chelicera, ventral; 77, Left male bulb, external; 78, Vulva, dorsal; 79, Vulva, ventral; 80, Vulva, lateral. Scale bars in mm.



Figures 81–86.—*Dysdera esquivei*, right male bulb and female spinnerets. 81, DD frontal; 82, DD external; 83, DD posterior; 84, P external; 85, Right ALS; 86, Right PLS.

end on DD internal tip; well-developed; located close to DD distal tip (Figs. 81–83); proximal border sharply decreasing; distal border stepped, upper tip not projected, rounded; external side hollowed. AC present. LF absent. L poorly developed; external border

not sclerotized, laterally slightly folded; distal border approximately parallel, not continuous, upper sheet slightly folded at middle (?). AL present, very poorly developed; proximal border in posterior view fused with DH. P (Fig. 84) fused to T; perpendicular to T in lateral

Table 7.—Intraspecific spination variability of *Dysdera gibbifera*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.1-2.1	0-1.0.0	0	1.0.0-1
Tibia 4 dorsal	0.0.1	1.0-1.1	1.0-1.0	1.0.1
Tibia 3 ventral	0-1.0.0	1.1.0-1	0	1.0-1.0
Tibia 4 ventral	1.1-2.1	1.0-1.0-1	0.1.0	1.0.1
	Number of rows		Number of spines	
Femur 3 dorsal	0		0	
Femur 4 dorsal	1		0-2	

view; lateral length from $\frac{2}{3}$ to as long as T width; ridge present, perpendicular to T, not expanded; upper margin smooth; distally slightly projected; back margin slightly folded towards internal side.

Paratype female: Figs. 78–80, 85, 86. All characters as in male except: Carapace 2.14 mm long; maximum width 1.58 mm; minimum width 0.98 mm.

Chelicerae 0.84 mm long; fang 0.6 mm. $B > D = M$ (slightly). Leg lengths of female described above: fe1 1.77 mm (all measurements in mm); pa1 1.19; ti1 1.39; me1 1.26; ta1 0.38; total 5.99; fe2 1.52; pa2 1.09; ti2 1.24; me2 1.14; ta2 0.38; total 5.37; fe3 1.19; pa3 0.66; ti3 1.21; me3 1.14; ta3 0.4; total 4.6; fe4 1.57; pa4 0.86; ti4 1.26; me4 1.52; ta4 0.4; total 5.61; relative length: $1 > 4 > 2 > 3$; palp: fe 0.94; pa 0.38; ti 0.38; ta 0.51; total 2.21. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; pa3 1-0 ventral; ti3 dorsal spines arranged in two bands: proximal 1-0.0.0; distal 1.0.0; ti3 ventral spines arranged in one band: distal 1.0.0; with two terminal spines. Fe4 dorsal spines in one row: 1; pa4 2-1 ventral; ti4 dorsal spines arranged in two bands: medial-proximal 1.0.1; distal 1.0.1; ti4 ventral spines arranged in four bands: proximal 1.0.0; medial-proximal 1.1.1; medial-distal 1.0.1; distal 1.0.1; without terminal spines.

Abdomen 2.7 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.05 mm long; medium thickness, curved, compressed (?), blunt, tip not enlarged; uniformly, scanty distributed. Vulva (Figs. 78–80) arch-like in dorsal view, frontally pointed; slightly wider than long; DF wide. MF poorly developed. VA frontal region completely sclerotized; posterior region sclerotized at anterior area. AVD hardly visible. S attachment not projected under VA; arms as long as DA, slightly curved;

tips not projected; neck as wide as arms. TB usual shape. ALS (Figs. 85, 86) with PS; remaining piriform spigots more external than MS, arranged in one row; 3 + 1 piriform gland spigots; PMS, PLS with fewer than 5 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 1.96–2.28 mm. Labrada specimen, carapace back margin slightly bilobulated. AME, PLE present, reduced to tiny whitish spots. Sternum lacking ornamentation. Chelicera dorsal relative size from $\frac{1}{4}$ – $\frac{2}{5}$ of carapace length. B larger than or

equal to D, larger than or equal to M. In general, cheliceral teeth are small. M closer to B. P very slightly toothed at distal tip (1 or 2 teeth). Spination variability in Table 6.

Additional material examined.—**TENERIFE:** *El Sauzal:* Cueva Labrada, 11 December 1984, 1♂ (J.J. Hernández, num. 2529 UL). *Icod de los Vinos:* Cueva Felipe Reventón, 3 March 1984, 1♂ paratype (G.I.E.T, num. 2526 UL); 20 June 1994, 1♂ (P. Oromí, num. 2801 UL); 22 April 1993, 1♀ (P. Oromí, num. 2548 UL); 18 May 1985, 1♂ (Hernández, Izquierdo & Medina, num. 2716 UL); ? May 1994, 1♂ (M. Arechavaleta, num. 2800 UL); ? May 1994, 1♀ (M. Arechavaleta, num. 2803 UL). *Cueva del Viento-Sobrado,* 23 March 1983, 1♂, 1juv. paratype (J.L. Martín, num. 2528 UL); 2 December 1992, 1♂ (I. Izquierdo, num. 2549 UL); ? May 1994, 1♂ (Piquetas, num. 2804 UL).

Distribution.—Tenerife endemic. Known from several lava tubes on the northern slope.

Dysdera gibbifera Wunderlich 1991
Figs. 87–95, Table 7

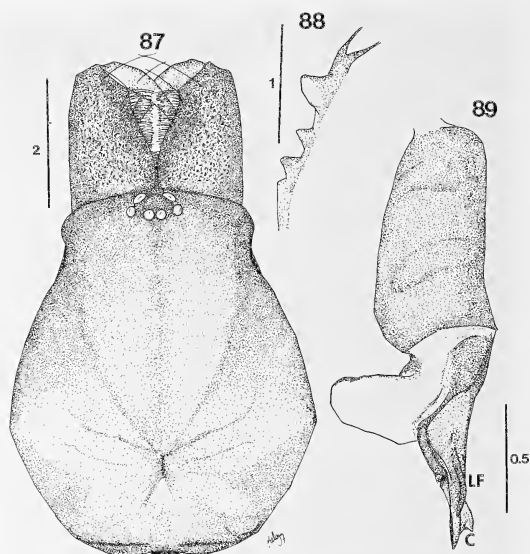
Dysdera gibbifera Wunderlich 1991: 293–294, figs. 35, 36, 38, 39 [♂] (♂; non♀, incorrect identification). Holotype male from MSS-3 Monte del Agua, Los Silos, Tenerife, Canary Islands; 10 July 1988, A.L. Medina leg.; num.T-H3-124;

Stored at UL. Examined. -Wunderlich 1991:284-287. -Arnedo & Ribera 1997.

Diagnosis.—*Dysdera gibbifera* can be distinguished from most of remaining Canarian *Dysdera* species by its large size (carapace 6.00 mm long). It differs from other large species such as *D. ambulotenta*, *D. hirgvan* Arnedo, Oromi & Ribera 1996, *D. insulana*, *D. labradaensis* and *D. longa* Wunderlich 1991, by its poorly spinated legs (Table 7).

Description.—*Holotype male*: Figs. 87–92. Carapace (Fig. 87) 5.81 mm long; maximum width 4.97 mm; minimum width 3.22 mm. Dark brownish-red, frontally darker, becoming lighter towards back; smooth with some black fine-textured granular material mainly at front. Frontal border roughly triangular, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders slightly convergent; sharpened at maximum dorsal width point, back lateral borders straight; back margin wide, straight. AME diameter 0.23 mm; PLE 0.21 mm; PME 0.2 mm; AME slightly back from frontal border, separated one from another about $\frac{1}{2}$ of diameter, far from PLE; PME about $\frac{1}{4}$ of diameter apart, about $\frac{3}{5}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base (rectangle-like); semicircular groove at tip. Sternum brownish-red, frontally darker, becoming lighter towards back; slightly wrinkled; covered in hairs mainly on margin.

Chelicerae (Fig. 88) 2.94 mm long, about $\frac{2}{3}$ of carapace length in dorsal view; fang medium-sized, 2.1 mm; basal segment dorsal, ventral side completely covered with piligerous granulations (small, dense). Chelicera inner groove short, about $\frac{1}{3}$ cheliceral length; armed with three teeth and lamina at base; D > B = M (large); D trapezoid, located near segment tip; B close to basal lamina; M close to B. Legs dark orange-colored. Lengths of male described above: fe1 5.6 mm (all measurements in mm); pa1 3.99; ti1 5.32; me1 4.9; ta1 0.91; total 19.81; fe2 5.11; pa2 3.57; ti2 4.83; me2 4.76; ta2 0.91; total 19.18; fe3 4.41; pa3 2.59; ti3 3.5; me3 4.41; ta3 0.91; total 15.82; fe4 5.67; pa4 3.01; ti4 4.62; me4 6.02; ta4 1.12; total 20.44; relative length: 4 > 1 > 2 > 3; palp: fe 3.5; pa 1.68; ti 1.75; ta 1.47; total 8.4. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands; proximal 1.1.1;

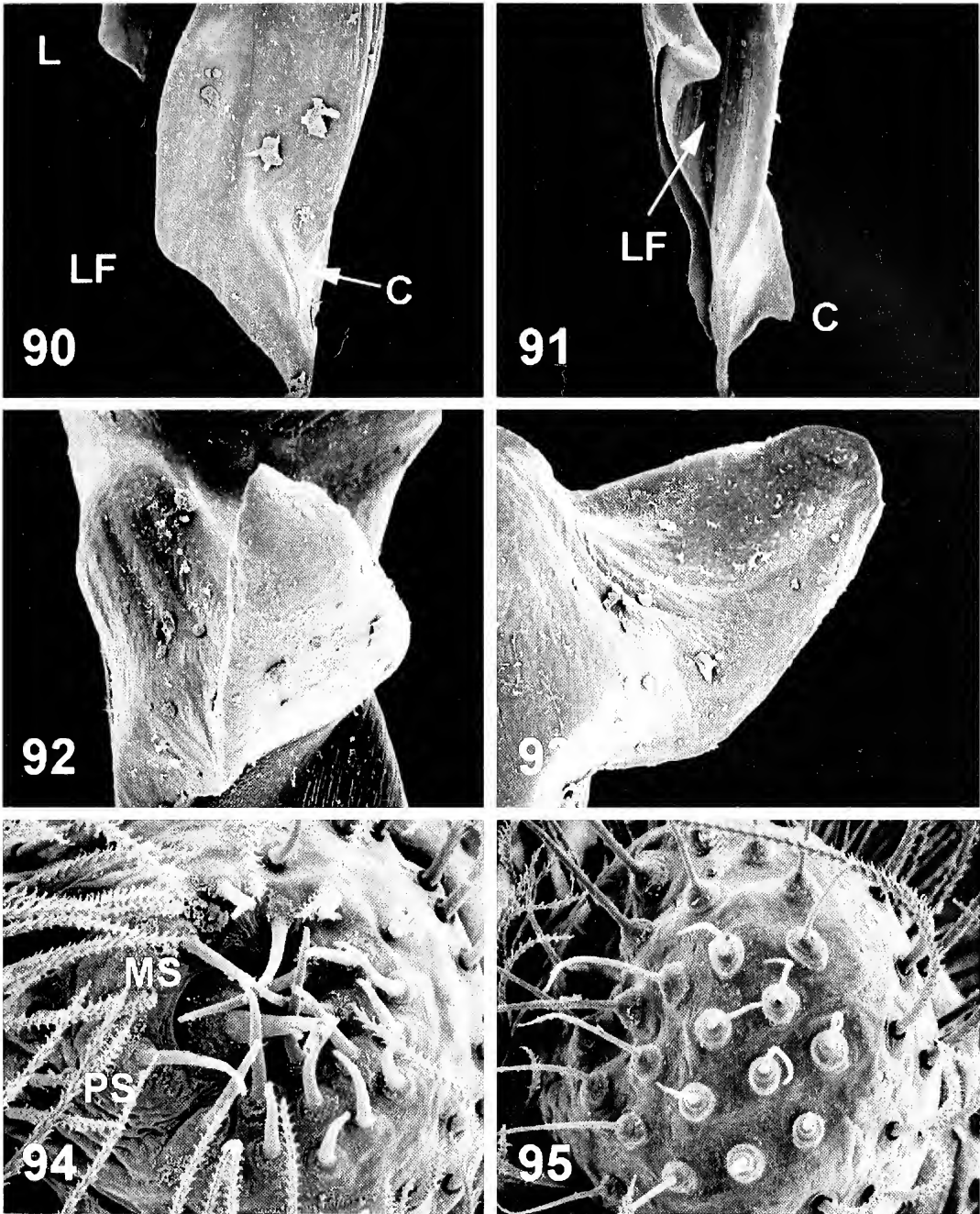


Figures 87–89.—*Dysdera gibbifera*. 87, Carapace, dorsal; 88, Left chelicera, ventral; 89, Right male bulb, external. Scale bars in mm.

distal 1.0.0; ti3 ventral spines arranged in three bands: proximal 1-0.0.0; medial-proximal 1.1.0; distal 1.0.0; with two terminal spines. Fe4 dorsal spines in one row: 0-1; ti4 dorsal spines arranged in four bands: proximal 0.0.1; medial-proximal 1.1.1; medial-distal 1.0.0; distal 1.0.1; ti4 ventral spines arranged in three bands: proximal 1.1.1; medial-proximal 1.1-0.0; distal 1.0-1.1; with two terminal spines. Dorsal side of frontal legs, ventral side of palp with a fine-textured, piligerous, granular surface. Claws with more than 20 teeth, slender, length twice claw width.

Abdomen 6.3 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.009–0.027 mm long (very small); medium thickness, roughly straight, not compressed, blunt, tip enlarged; uniformly, scanty distributed. ALS (Figs. 94, 95) with PS; remaining piriform spigots no more external than MS, arranged in three rows; 18 + 1 piriform gland spigots; PMS, PLS with more than 20 aciniform gland spigots.

Male bulb: (Fig. 89). T slightly longer than DD, or T as long as DD; external, internal distal border sloped backwards. DD not bent, same T axis in lateral view; internal distal border not expanded. ES wider, more sclerotized than IS; IS continuous to tip. DD tip (Figs. 90–92) straight in lateral view. C present, short; distal end on DD internal tip; well-de-



Figures 90–95.—*Dysdera gibbifera*, right male bulb and spinnerets. 90, DD frontal; 91, DD external; 92, DD posterior; 93, P external; 94, Right ALS; 95, Right PLS.

veloped; located far from DD distal tip; proximal border sharply decreasing; distal border sloping on its base, upper tip not projected, pointed; external side hollowed (slightly). AC absent. LF present; distally not projected; well-developed. L well-developed; external

border sclerotized, laterally markedly folded backwards; distal border divergent, continuous. AL absent. P (Fig. 93) fused to T; markedly sloped on its proximal part, perpendicular on distal; lateral length as long as or longer than T width; ridge present, not sclerotized,

perpendicular to T, distinctly expanded, rounded; upper margin smooth; not distally projected; back margin not folded.

Female: Unknown.

Intraspecific variation.—Male cephalothorax ranges in length from 5.81–7.00 mm. Carapace very slightly wrinkled. AME separation from $\frac{1}{2}$ – $\frac{2}{3}$ of diameter. Sternum hardly wrinkled. P distally slightly toothed. Spination variability in Table 7.

Additional material examined.—**TENERIFE:** *Icod de los Vinos*: Cueva de Felipe Reventón; 17 February 1985, 1♂ (J.J. Hernández & A.L. Medina, num. 2709 UL). *Los Silos*: Monte del Agua, 6 July 1990, 1♂ (C.G. Campos, num. 2779 UL).

Distribution.—Tenerifean endemic. Known from two localities at westernmost part of the northern slope, including Teno.

Comments.—The study of the female specimens assigned to this species in the original description (Wunderlich 1991) shows that they actually belonged to a different species, the already identified Tenerifean species *D. insulana* (Arnedo & Ribera 1997). Therefore, the female of this species is currently unknown.

Dysdera gollumi Ribera & Arnedo 1994
Figs. 118–119

Dysdera gollumi Ribera & Arnedo 1994: 115–119, fig. 1–3 [♀]. Holotype female from Cueva de Los Roques, La Orotava, Tenerife, Canary Islands; 27 October 1991, C. Ribera leg.; num. 2567; Stored at UB. Examined.

Diagnosis.—*Dysdera gollumi* can be distinguished from most of the Canarian *Dysdera* species by the eye reduction, spineless legs and small size (carapace \leq 2.00 mm long). It differs from the other small and troglomorphic species, *D. esquiveli* and *D. hernandezi* new species, by its markedly foveate carapace.

Description.—*Holotype female*: Carapace 2.05 mm long; maximum width 1.49 mm; minimum width 0.79 mm. Dark reddish-brown, darkened at borders; heavily wrinkled, foveate, covered with small black 'granules'. Frontal border roughly triangular, markedly smaller than $\frac{1}{2}$ carapace length; anterior lateral borders divergent; rounded at maximum dorsal width point, back lateral borders rounded; back margin projected. PME, PLE lost; AME markedly reduced (tiny bright spots); AME diameter 0.022 mm; AME separation

0.12 mm. Labium trapezoid-shaped, base wider than distal part; as long as wide at base (triangle-like); semicircular groove at tip. Sternum orange-brown, darkened on borders; heavily wrinkled; covered in hairs mainly on margin.

Chelicerae 0.63 mm long, about $\frac{1}{4}$ of carapace length in dorsal view; fang short, 0.44 mm; basal segment proximal dorsal side scantily covered with large piligerous granulations. Chelicera inner groove medium-size, about $\frac{2}{5}$ cheliceral length; armed with three teeth and lamina at base; $D = B > M$ (very slightly); D triangular, located roughly at center of groove; B close to basal lamina; M at middle of B and D. Legs bicolored, darker on proximal border, becoming lighter distally. Lengths of female described above: fe1 2.1 mm (all measurements in mm); pa1 1.03; ti1 1.96; me1 2; ta1 0.51; total 7.6; fe2 1.72; pa2 1.03; ti2 1.68; me2 1.77; ta2 0.51; total 6.71; fe3 1.44; pa3 0.7; ti3 1.12; me3 1.49; ta3 0.42; total 5.17; fe4 1.91; pa4 0.98; ti4 1.58; me4 2.05; ta4 0.56; total 7.08; relative length $1 > 4 > 2 > 3$; palp: fe 0.76; pa 0.36; ti 0.41; ta 0.61; total 2.14. Spination: spineless. Dorsal side of frontal legs smooth; ventral side of palp covered with hairs, lacking a granular surface. Claws with 8 teeth or less, robust, hardly larger than claw width.

Abdomen 3.26 mm long; whitish; globular. Abdominal dorsal hairs 0.054 mm long; thin, curved, not compressed, blunt, tip not enlarged; uniformly, scantily distributed. Vulva arch-like in dorsal view, frontally rounded; slightly wider than long; DF wide. MF poorly developed. VA frontal region completely sclerotized; posterior region sclerotized at anterior area. AVD hardly visible. S attachment projected under VA; arms slightly shorter than DA, slightly curved; tips not projected; neck as wide as arms. TB usual shape. ALS (Figs. 118, 119) with PS; remaining piriform spigots more external than MS, arranged in one row; 5 + 1 piriform gland spigots; PMS, PLS with fewer than 5 aciniform gland spigots.

Male: Unknown.

Intraspecific variation.—Female cephalothorax ranges in length from 1.82–2.05 mm. Cheliceral teeth small, $B > M > D$. Chelicera groove short. Vulva frontally pointed, in dorsal view. As wide as long.

Additional material examined.—**TENERIFE:**

Table 8.—Intraspecific spination variability of *Dysdera guayota*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.1-2.1	0	0	1.0.1
Tibia 4 dorsal	0.0.0-1	1.1.1	0	1.0.1
Tibia 3 ventral	1.1-2.0	0	0	1.0-1.0
Tibia 4 ventral	1.1.1	0-1.1.0	0	0-1.0.0-1
	Number of rows		Number of spines	
Femur 1 dorsal	1		1-2	
Femur 2 dorsal	1		2-3	
Femur 3 dorsal	2		1-10/0-9	
Femur 4 dorsal	2		1-4/4-7	

La Orotava: Cueva de Los Roques, 28 December 1982, 1juv. (J.L. Martín, num. 2537 UL); ? November 1995, 1♀ (P. Oromí, num. 2966 UB).

Distribution.—Tenerifean endemic. Known from a single lava tube, located at dry, middle-southern slope.

Comments.—Drawings of carapace, chelicera and vulva of this species have been published elsewhere (Ribera & Arnedo 1994). In the present article, SEM photographs of spinerets are provided for the first time.

Dysdera guayota new species
Figs. 96–107, Table 8

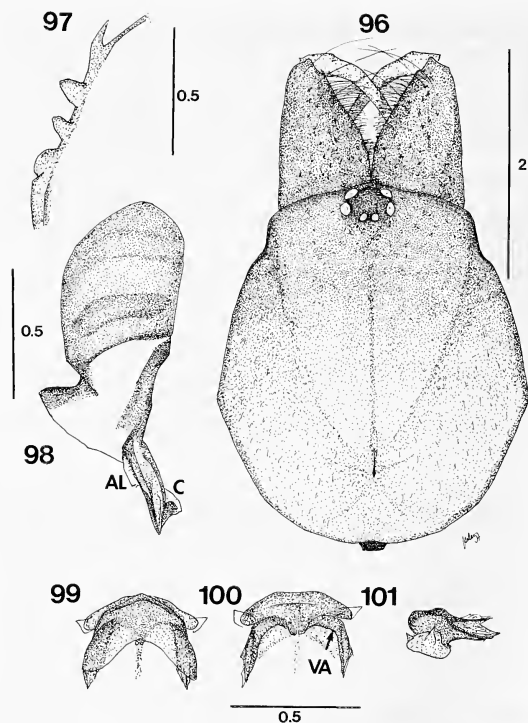
Types.—Holotype male from Las Cañadas, La Orotava, Tenerife, Canary Islands; 22 October 1995, A. Camacho leg.; num. 3153. Stored at UB. Paratype female from Las Cañadas del Teide, close to crossroads to Vilaflor, Adeje, Tenerife, Canary Islands; 29 November 1993, Arnedo & Fluhr leg.; num. 4826. Stored at UB.

Etymology.—The name in apposition of this species means ‘devil’ in the language of the ‘guanches,’ the ancient aboriginal inhabitants of Tenerife.

Diagnosis.—*Dysdera guayota* new species can be distinguished from all other Canarian *Dysdera* species except *D. chioensis*, *D. labradaensis* and *D. lancerotensis* by having spines on anterior femora (legs 1, 2). Males differs from *D. lancerotensis* by lacking hook-like apophysis in frontal-distal tip of bulb distal division (DD) and bulb posterior apophysis (P) fused to tegulum (T), and females by the sclerotization of frontal part of vulva ventral (VA). It differs from *D. labradaensis* and *D. chioensis* by not showing eye reduction.

Description.—*Holotype male*: Figs. 96–98, 102–105. Carapace (Fig. 96) 3.63 mm long; maximum width 3.17 mm; minimum width 2.1 mm. Brownish-orange, frontally darker, becoming lighter towards back; smooth with some small black ‘granules’ mainly at front; hairy, covered with black hairs mainly at lateral and back borders. Frontal border roughly straight, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders slightly convergent; sharpened at maximum dorsal width point, back lateral borders straight; back margin wide, straight. AME diameter 0.16 mm; PLE 0.12 mm; PME 0.11 mm; AME slightly back from frontal border, separated one from another about 1 diameter or more, close to PLE; PME about $\frac{1}{4}$ of diameter apart, about $\frac{2}{5}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base (rectangle-like); semicircular groove at tip. Sternum orange, uniformly distributed; very slightly wrinkled, mainly between legs, frontal border; uniformly covered in slender black hairs.

Chelicerae (Fig. 97) 1.72 mm long, about $\frac{1}{3}$ of carapace length in dorsal view; fang medium-sized, 1.12 mm; basal segment dorsal side completely covered with piligerous granulations, ventral side smooth. Chelicera inner groove short, about $\frac{1}{3}$ cheliceral length; armed with three teeth and lamina at base; $D > B > M$ (all large, B broken?); D trapezoid, located near segment tip; B close to basal lamina; M close to B. Front legs dark orange, back legs yellow. Lengths of male described above: fe1 2.98 mm (all measurements in mm); pa1 1.82; ti1 2.61; me1 2.61; ta1 0.6; total 10.62; fe2 2.65; pa2 1.68; ti2 2.56; me2 2.23; ta2 0.6;



Figures 96–101.—*Dysdera guayota* new species. 96, Carapace, dorsal; 97, Left chelicera, ventral; 98, Right male bulb, external; 99, Vulva, dorsal; 100, Vulva, ventral; 101, Vulva, lateral. Scale bars in mm.

total 9.72; fe3 2.1; pa3 1.21; ti3 1.68; me3 2.05; ta3 0.56; total 7.6; fe4 2.7; pa4 1.44; ti4 2.14; me4 2.56; ta4 0.65; total 9.49; relative length: $1 > 2 > 4 > 3$; palp: fe 1.79; pa 0.88; ti 0.7; ta 0.93; total 4.3. Spination: palp spineless. Fe1 3-2 distal, anterior margin. Fe2 2-3 distal, anterior margin. Fe3 dorsal spines in two rows: anterior 9-10; posterior 5-4; ti3 dorsal spines arranged in two bands: proximal 1.1.1; distal 1.0.1; ti3 ventral spines arranged in two bands: proximal 1.1.0; distal 1.0.0; with one terminal spine on anterior margin. Fe4 dorsal spines in two rows: anterior 4-2; posterior 7-5; ti4 dorsal spines arranged in three bands: proximal 0.0.1; medial-proximal 1.1.1; distal 1.0.1; ti4 ventral spines arranged in three bands: proximal 1.1.1; medial-proximal 0.1.0; distal 1.0.1; with two terminal spines. Dorsal side of frontal legs, ventral side of palp covered with hairs. Claws with 8 teeth or less; robust, hardly larger than claw width.

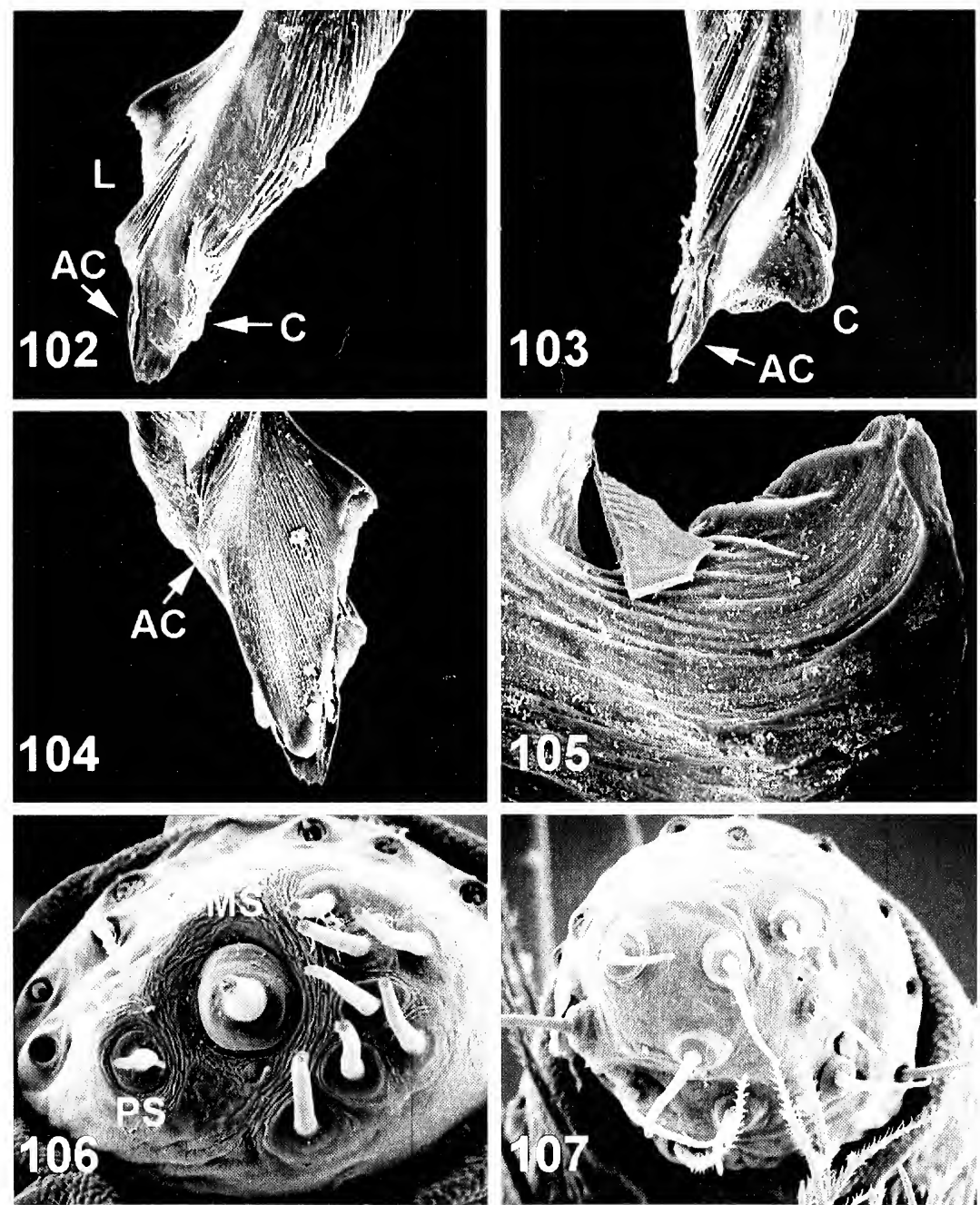
Abdomen 3.59 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.09 mm long;

thick, slightly curved, compressed, blunt, tip not enlarged; uniformly, thickly distributed.

Male bulb (Fig. 98): T as long as DD; external, internal distal border sloped backwards. DD proximally bent about 45° in lateral view; internal distal border not expanded. IS and ES equally developed; IS truncated at DD middle part. DD tip (Figs. 102–104) sloped towards back in lateral view. C present, short; distal end on DD internal tip; well-developed; located close to DD distal tip; proximal border sharply decreasing; distal border stepped, upper tip projected, pointed; external side hollowed. AC present. LF absent. L well-developed; external border not sclerotized, laterally slightly folded; distal border divergent, not continuous; upper sheet strongly fold at middle. AL present, well-developed; proximal border in posterior view toothed on its internal half-part. P (Fig. 105) fused to T; perpendicular to T in lateral view; lateral length from $\frac{1}{2}$ – $\frac{2}{3}$ of T width; ridge present, perpendicular to T, not expanded; upper margin markedly toothed, along its extent, few teeth; not distally projected; back margin not folded.

Paratype female: Figs. 99–101, 106, 107. All characters as in male except: Carapace 3.36 mm long; maximum width 2.75 mm; minimum width 1.86 mm. Orange. AME diameter 0.18 mm; PLE 0.12 mm; PME 0.12 mm; PME $\frac{3}{5}$ diameter from PLE. Sternum yellow, frontally darker, becoming lighter towards back; smooth.

Chelicerae 1.75 mm long; fang 0.31 mm; basal segment proximal dorsal side scanty covered with piligerous granulations. $B > D > M$ (B, D similar). Legs yellow. Lengths of female described above: fe1 2.33 mm (all measurements in mm); pa1 1.49; ti1 1.86; me1 1.4; ta1 0.46; total 7.54; fe2 2.14; pa2 1.4; ti2 1.86; me2 1.58; ta2 0.46; total 7.44; fe3 1.72; pa3 1.02; ti3 1.35; me3 1.58; ta3 0.46; total 6.13; fe4 2.37; pa4 1.26; ti4 1.86; me4 2.1; ta4 0.56; total 8.15; relative length $4 > 1 > 2 > 3$; palp: fe 1.49; pa 0.64; ti 0.51; ta 0.74; total 3.38. Spination: palp spineless. Fe1: 2 distal, anterior margin. Fe2: 2-1 distal, anterior margin. Fe3 dorsal spines in one row: 1 (medial frontal); ti3 dorsal spines arranged in two bands: proximal 1.1.1; distal 1.0.1; ti3 ventral spines arranged in two bands: proximal 1.1.0; distal 1.0.0; with two terminal spines. Fe4 dorsal spines in two rows: anterior 1; posterior 4; ti4 dorsal spines arranged in



Figures 102–107.—*Dysdera guayota* new species, right male bulb and female spinnerets. 102, DD frontal; 103, DD external; 104, DD posterior; 105, P internal; 106, Right ALS; 107, Right PLS.

two bands: medial-proximal 1.1.1; distal 1.0.1; ti4 ventral spines arranged in three bands: proximal 1.1.1; medial-proximal 0.1.0; distal 1-0.0.0-1; with two terminal spines. Dorsal side of frontal legs smooth.

Abdomen 3.59 mm long; whitish; cylindri-

cal. Abdominal dorsal hairs 0.162 mm long; medium thickness, curved, compressed, pointed; uniformly, thickly distributed. Vulva (Figs. 99–101) arch-like in dorsal view, frontally rounded; slightly wider than long; DF wide. MF poorly developed. VA frontal re-

Table 9.—Intraspecific spination variability of *Dysdera hernandezi*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	0	0	0	1.0.0
Tibia 4 dorsal	0	0	0	0.0.1
Tibia 3 ventral	0	0	0	0
Tibia 4 ventral	1.0-1.0	0	0	1.0.0

gion completely sclerotized; posterior region sclerotized at anterior area. AVD hardly visible. S attachment projected under VA; arms as long as DA, slightly curved; tips dorsally projected; neck as wide as arms. TB usual shape. ALS (Figs. 106, 107) with PS; remaining piriform spigots more external than MS, arranged in two rows; 7 + 1 piriform gland spigots; PMS, PLS with 5–10 aciniform gland spigots.

Intraspecific variation.—Female cephalothorax ranges in length from 3.15–3.36 mm. PLE-PME from $\frac{2}{3}$ –1 diameter. Spination variability in Table 8.

Paratypes.—**TENERIFE:** *Adeje:* Las Cañadas, close to crossroads to Vilaflor; 1juv.; November 1993, Arnedo & Fluhr leg.; num. 4815 (T10); Stored at UB. Roque del Conde; 1juv. paratype; 16 March 1996, P. Oromí leg.; num. 3170; Stored at UL. Arona: Los Cristianos; 1♀ paratype; 20 January 1996, Oromí leg.; num. 3094; Stored at UL.

Distribution.—Tenerifean endemic. Known from several localities on dry, south-western slope.

Dysdera hernandezi new species

Figs. 108–112, 120, 121, Table 9

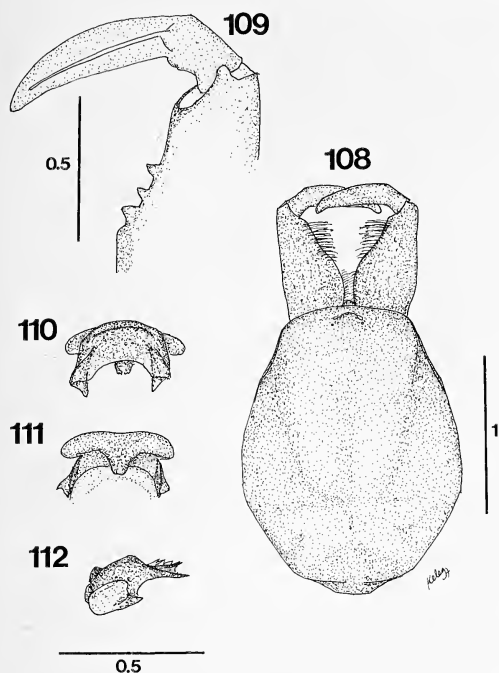
Types.—Holotype female from Cueva Labrada, El Sauzal, Tenerife; 11 December 1984, J.J. Hernández leg.; num. 3214; Stored at UL.

Etymology.—This species is dedicated to the late Juan José Hernández Pacheco, enthusiastic Canarian biospeleologist and collector of the only two known specimens of this species.

Diagnosis.—*Dysdera hernandezi* new species can be distinguished from most of the Canarian *Dysdera* by its flat and enlarged cheliceral fang (Fig. 109). A very similar fang shape is also present in *D. ramblae* Arnedo, Oromí & Ribera 1996 from La Gomera, from which differs by the smooth carapace, smaller size and eye reduction.

Description.—*Holotype female:* Figs. 108–112, 120, 121. Carapace (Fig. 108) 1.91 mm long; maximum width 1.4 mm; minimum width 0.9 mm. Pale orange, uniformly distributed; very slightly foveate at borders, wrinkled at middle, covered with tiny granulations. Frontal border roughly round, markedly smaller than $\frac{1}{2}$ carapace length; anterior lateral borders divergent; rounded at maximum dorsal width point, back lateral borders straight; back margin projected. PME lost; AME, PLE markedly reduced (bright tiny spots); AME diameter 0.018 mm; PLE 0.018 mm; AME separation 0.16 mm; AME-PLE separation 0.018 mm. Labium trapezoid-shaped, base wider than distal part; as long as wide at base (triangle-like); semicircular groove at tip. Sternum pale orange, uniformly distributed; slightly wrinkled; covered in hairs mainly on margin.

Chelicerae (Fig. 109) 0.79 mm long, about $\frac{1}{3}$ of carapace length in dorsal view; fang medium-sized, 0.65 mm; enlarged on middle part; basal segment smooth, with no granulations. Chelicera inner groove medium-size, about $\frac{2}{5}$ cheliceral length; armed with three teeth and lamina at base; B > D > M (not very different, small); D triangular, located roughly at center of groove; B close to basal lamina; M close to B. Legs pale yellow. Lengths of female described above: fe1 1.42 mm (all measurements in mm); pa1 0.98; ti1 1.21; me1 1.21; ta1 0.37; total 5.2; fe2 1.35; pa2 0.93; ti2 1.16; me2 1.16; ta2 0.35; total 4.95; fe3 1.02; pa3 0.61; ti3 0.84; me3 0.98; ta3 0.32; total 3.77; fe4 1.35; pa4 0.74; ti4 1.12; me4 1.26; ta4 0.37; total 4.47; relative length 1 > 2 > 4 > 3; palp: fe 0.79; pa 0.42; ti 0.37; ta 0.51; total 2.09. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in one band; distal 1.0.0; ti3 ventral spines spineless; with one terminal spine on anterior margin. Fe4 dorsal



Figures 108–112.—*Dysdera hernandezi* new species. 108, Carapace, dorsal; 109, Left chelicera, ventral; 110, Vulva, dorsal; 111, Vulva, ventral; 112, Vulva, lateral. Scale bars in mm.

spineless; ti4 dorsal spines arranged in one band: distal 0.0.1; ti4 ventral spines arranged in two bands: proximal 1.1-0.0; distal 1.0.0; with two terminal spines. Dorsal side of frontal legs smooth; ventral side of palp covered with hairs, lacking a granular surface; long, spine-like hairs on posterior ti, fe (mainly ventral). Claws with 10–14 teeth, length twice claw width.

Abdomen 2.37 mm long; whitish; globular. Abdominal dorsal hairs 0.036 mm long; thin, curved, not compressed, blunt, tip not enlarged; uniformly, scantily distributed. Vulva (Figs. 110–112) DA arch-like in dorsal view, frontally rounded; slightly wider than long; DF wide. MF poorly developed. VA frontal region completely sclerotized; posterior region sclerotized at anterior area. AVD hardly visible. S attachment not projected under VA; arms as long as DA, straight; tips not projected; neck as wide as arms. TB usual shape. ALS (Figs. 120, 121) with PS; remaining piriform spigots more external than MS, arranged in one row; 4 + 1 piriform gland spigots; PMS, PLS with 5–10 aciniform gland spigots.

Male: Unknown.

Intraspecific variation.—Female cephalothorax ranges in length from 1.91–2.14 mm. Carapace frontal width about $\frac{1}{2}$ of its length. Sternum wrinkled. Spination variability in Table 9.

Paratype.—**TENERIFE:** *El Sauzal:* Cueva Labrada; 1 ♀ paratype; 22 November 1984, J.J. Hernández leg.; num. 2585; Stored at UB.

Distribution.—Tenerifean endemic. Known from a single lava tube, located on middle-northern slope.

Dysdera iguanensis Wunderlich 1987

Dysdera iguanensis Wunderlich 1987: 57–58, Figs. 2–6 [♂]. -Wunderlich 1991: 294–295, fig. 41 [♀]. -Wunderlich 1991: 284–287. -Arnedo et al. 1996: 244, fig. 1F [♂]. -Arnedo & Ribera 1997.

Distribution.—Canarian endemic, known from Tenerife and a single location in Gran Canaria. In Tenerife it is an abundant species, spread through several localities on northern slope, including Anaga and Teno massifs.

Comments.—A complete redescription of this species has been published elsewhere (Arnedo & Ribera 1997).

Dysdera insulana Simon 1883

Dysdera insulana Simon 1883: 294–295, fig. 19 [♂] (♂, non ♀). -Simon 1907: 257–258, fig. A [♂]. -Strand 1911: 190. -Reimoser 1919. -Denis 1941: 108. -Denis 1953: 2. -Schmidt 1973: 360–361. -Wunderlich 1991: 67, 296. -Arnedo et al. 1996: 271–272. -Arnedo & Ribera 1997.

Distribution.—Canarian endemic, known from Tenerife and a single location in Gran Canaria. In Tenerife, known from several localities restricted to Anaga and closer location, formerly occupied by low-elevation laurel forest.

Comments.—A complete redescription of this species has been published elsewhere (Arnedo & Ribera 1997).

Dysdera labradaensis Wunderlich 1991 Figs. 113–117, 122, 123, Table 10

D. labradaensis Wunderlich 1991: 296, figs. 47–49 [♀]. Holotype female from Cueva Labrada, El Sauzal, Tenerife, Canary Islands; 12 September 1984, G.I.E.T. leg.; num. T-CL-59; Stored at UL. Examined. -Wunderlich 1991: 284–287.

Diagnosis.—*Dysdera labradaensis* differs from similar and sympatric species *D. ambu-*

Table 10.—Intraspecific spination variability of *Dysdera labradaensis*.

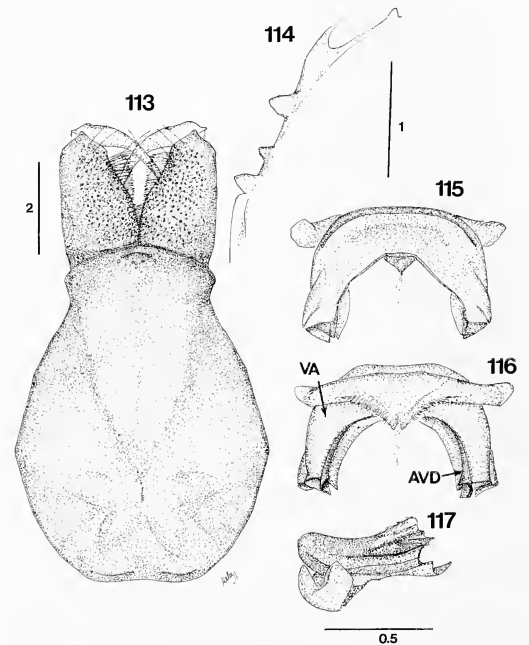
	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	0-1.0-1.0-1	0-1.0-2.0-1	1.0-1.0-1	1.0-1.1
Tibia 4 dorsal	1.2.1-2	1.1-3.1	1.0-1.1	1.1.1
Tibia 3 ventral	1.1.1	1.1.1	0	1.1.1
Tibia 4 ventral	0-1.0-2.1-2	1.1.1	1.1.1	1.1.1
Number of spines				
Patella 3 ventral	0-1			
Patella 4 ventral	0-1			
Number of rows		Number of spines		
Femur 1 frontal	1	3		
Femur 2 frontal	1	1-2		
Femur 3 dorsal	2	3-4(distal)/2-3(proximal)		
Femur 4 dorsal	2	6-8(distal)/2-3(proximal)		

lotenta by presence of six eyes, spinated anterior femora and presence of a ridge on vulva ventral arch (VA). It can be distinguished from other species with a ridge on ventral arch (Grancanarian *D. arabisenen* Arnedo & Ribera 1997, *D. tibicena* Arnedo & Ribera 1997 and Tenerifean *D. iguanensis*, *D. montaneten-*

sis) by possessing a ridge longer than the ventral arch (Fig. 116).

Description.—*Holotype female*: Figs. 113–117, 122, 123. Carapace (Fig. 113) 8.33 mm long; maximum width 6.58 mm; minimum width 3.78 mm. Brownish-orange, frontally darker, becoming lighter towards back; smooth with some small black ‘granules’ mainly at front; hairy, covered with black hairs mainly at lateral and back borders. Frontal border roughly straight, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders slightly convergent; sharpened at maximum dorsal width point, back lateral borders straight; back margin wide, straight. Eyes markedly reduced in size; AME diameter 0.16 mm; PLE 0.14 mm; PME 0.12 mm; AME separation 0.52 mm; AME-PLE separation 0.07 mm; PLE-PME separation 0.2 mm; PME separation 0.09 mm. Labium trapezoid-shaped, base wider than distal part; longer than wide at base (rectangle-like); semicircular groove at tip. Sternum orange, frontally darker, becoming lighter towards back; very slightly wrinkled, mainly between legs, frontal border; uniformly covered in slender black hairs.

Chelicerae (Fig. 114) 3.22 mm long, about $\frac{1}{3}$ of carapace length in dorsal view; fang medium-sized, 2.52 mm; basal segment dorsal, ventral side completely covered with piligerous granulations (small, dense). Chelicera inner groove short, about $\frac{1}{3}$ cheliceral length; armed with three teeth and lamina at base; D = B > M (large, similar in size); D trapezoid,



Figures 113–117.—*Dysdera labradaensis*. 113, Carapace, dorsal; 114, Left chelicera, ventral; 115, Vulva, dorsal; 116, Vulva, ventral; 117, Vulva, lateral. Scale bars in mm.

located roughly at center of groove; B close to basal lamina; M close to B. Legs dark orange-colored. Lengths of female described above: fe1 7.7 mm (all measurements in mm); pa1 4.9; ti1 7; me1 7.21; ta1 1.12; total 27.93; fe2 7.28; pa2 4.69; ti2 6.72; me2 7; ta2 1.12; total 26.71; fe3 6.3; pa3 3.43; ti3 4.9; me3 6.51; ta3 1.19; total 22.33; fe4 8.4; pa4 4.2; ti4 7.14; me4 9.45; ta4 1.33; total 3.52; relative length $4 > 1 > 2 > 3$; palp: fe 3.92; pa 2.1; ti 2.03; ta 2.38; total 10.43. Spination: palp spineless. Fe1: 3 distal, anterior margin. Fe2: 1-2 distal, anterior margin. Fe3 dorsal spines in two rows: anterior 4-3 (distal); posterior 2-3 (proximal); pa3 1-0 ventral; ti3 dorsal spines arranged in four bands: proximal 1-0.0.0; medial-proximal 1.2-1.1; medial-distal 1.1.0-1; distal 1.0.1; ti3 ventral spines arranged in three bands: proximal 1.1.1; medial-proximal 1.1.1; distal 1.1.1; with two terminal spines. Fe4 dorsal spines in two rows: anterior 5-6 (2 distal); posterior 2-3; ti4 dorsal spines arranged in four bands: proximal 1.2.1; medial-proximal 1.2.1; medial-distal 1.1.1; distal 1.1.1; ti4 ventral spines arranged in four bands: proximal 1.1.2-1; medial-proximal 0-1.0-1.1; medial-distal 1.1.1; distal 2-1.1.1; with two terminal spines. Dorsal side of frontal legs, ventral side of palp slightly covered with a fine-textured piligerous granular surface. Claws with more than 20 teeth, length twice claw width.

Abdomen 9.8 mm long; cream-colored; cylindrical. Abdominal dorsal hairs 0.036–0.072 mm long (small, variable); medium thickness, roughly straight, not compressed, blunt, tip enlarged; uniformly, scantily distributed. Vulva (Figs. 115–117) rectangle-like in dorsal view, frontally rounded; twice as wide as long; DF wide. MF well-developed; markedly sclerotized along its extent. VA frontal region completely sclerotized; posterior region sclerotized except for most internal area; sclerotized ridge at ventral VA external margin, longer than VA, fused to VA along its extent, back ends bent to internal side. AVD clearly recognizable. S attachment projected under VA; arms as long as DA, slightly curved; ends projected anteriors; neck as wide as arms. TB usual shape. ALS (Figs. 122, 123) with PS; remaining piriform spigots more external than MS, arranged in three rows; more than 20

piriform gland spigots; PMS, PLS with 10–15 aciniform gland spigots.

Male: Unknown.

Intraspecific variation.—Female cephalothorax ranges in length from 7.00–8.33 mm. B larger than M. Spination variability in Table 10.

Additional material examined.—**TENERIFE:** *Icod de los Vinos*: Cueva del Viento-Sobrado, 30 November 1980, 1juv. (J.L. Martín, num. 2522 UL); 5 April 1981, 1juv. (J.L. Martín, num. 2515 UL); 17 September 1990, 1juv. (J.J. Hernández, num. 2746 UL); 17 September 1990, 1juv. (J.J. Hernández, num. 2747 UL); ? May 1994, 1juv. (J. Sala, num. 2802 UL). *La Orotava*: Cueva del Buncio, 4 August 1985, 1juv. (Martín & Machado, num. 2743 UL). *El Sauzal*: Cueva Labrada, 21 March 1983, 1♀, some remains, (J.L. Martín, num. 2531 UL); 28 June 1986, 1♀ (P. Oromí, num. 2513 UL).

Distribution.—Tenerifean endemic. Known from several lava tubes located on northern slope of the island.

Dysdera levipes Wunderlich 1987

Dysdera levipes Wunderlich 1987: 59–60, fig. 19–22 [♂]. -Wunderlich 1991: 284–287. -Arnedo et al. 1996: 258–261, figs. 14A–F, 15A–D, 16A–C [♂, ♀]. -Arnedo & Ribera 1997.

Dysdera multipilosa Wunderlich 1991: 301–302, figs. 68–71 [♀].

Distribution.—Canarian endemic, found in Tenerife, La Gomera and Gran Canaria. In Tenerife has been reported from two localities on the northern slope and a single locality on middle-southern slope.

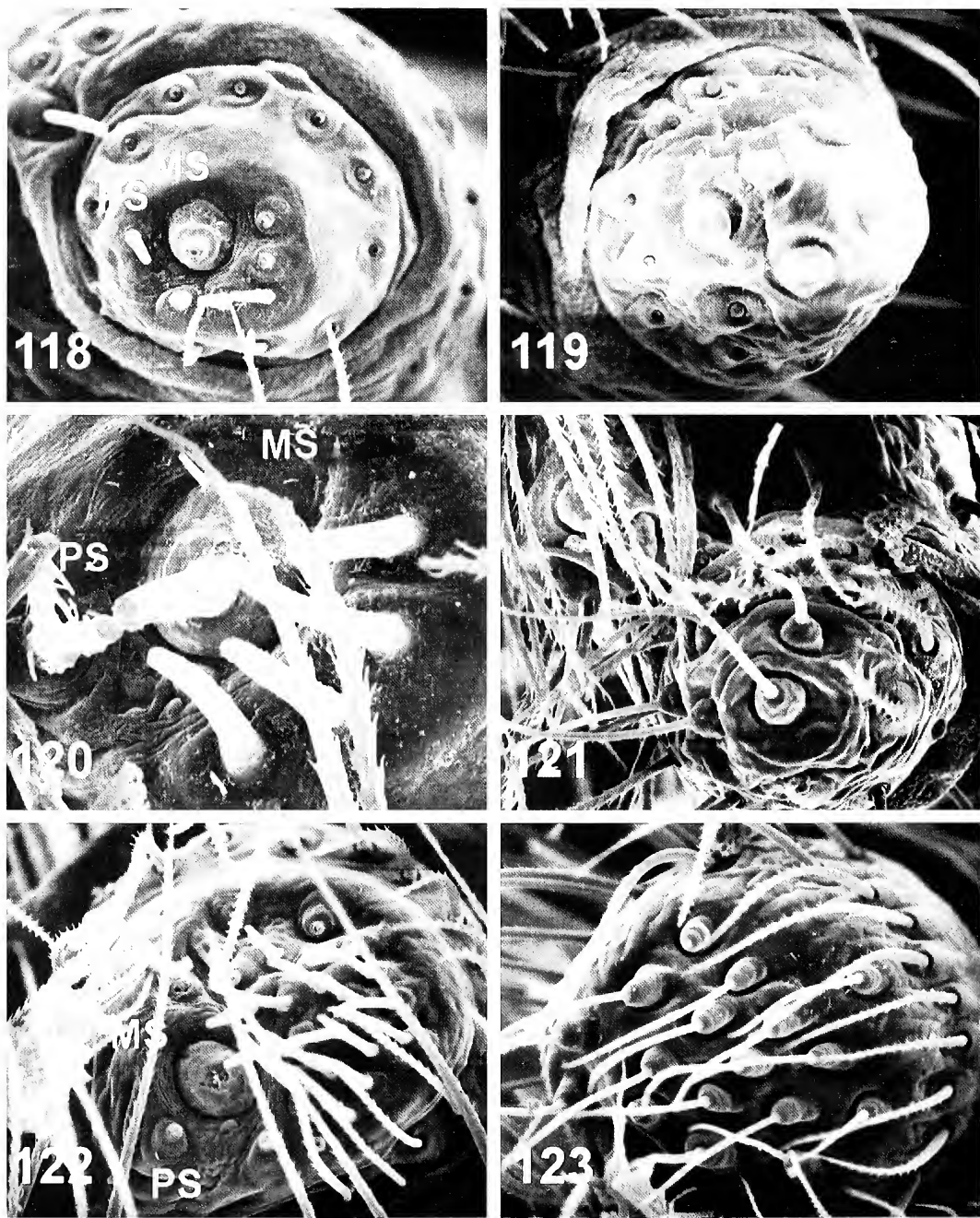
Comments.—A complete redescription of this species has been published elsewhere (Arnedo et al. 1996). *D. levipes* is the only endemic species reported from three different islands: La Gomera, Tenerife and Gran Canaria (a single specimen).

Dysdera macra Simon 1883

Figs. 124–136, Table 11

Dysdera macra Simon 1883: 295–296, fig. 18 [♂] (♂, non ♀). Neotype male, by present designation, from Monte de Santa Ursula, Santa Ursula, Tenerife, Canary Islands; 27 February 1997, P. Oromí leg.; num. 3206; Stored at UB. -Simon 1907: 256–267, 259–260; fig. 3, dorsal [♂]. -Strand 1911: 189. -Reimoser 1919: 200. -Denis 1941: 108. -Schmidt 1973: 360–361. -Arnedo et al. 1996: 272.

D. teneriffensis Strand 1908: 772 [♀]. Holotype fe-



Figures 118–123.—Spinnerets. 118, 119, *Dysdera gollumi*. 118, Right ALS; 119, Right PLS. 120–121, *Dysdera hernandezi* new species. 120, Right ALS; 121, Right PLS. 122–123, *Dysdera labradaensis*. 122, Right ALS; 123, Right PLS.

male from Aguamansa (Aqua Manza), La Orotava, Tenerife, Canary Islands; unknown data, unknown leg.. Probably lost. Not examined. -Wunderlich 1991: 283. New synonymy.
D. pergrada Wunderlich 1991: 305–306, figs. 83–91 [♂,♀]. Holotype male from close to La Oro-

tava, La Orotava, Tenerife, Canary Islands; in II, M. Knösel leg.; num. 37163; Stored at SMF Examined. New synonymy.
D. pseudopergrada Wunderlich 1991: 306, figs. 94–97 [♂,♀]. Holotype male from Barranco del Infierno, Adeje, Tenerife, Canary Islands; in II,

Table 11.—Intraspecific spination variability of *Dysdera macra* (hardly distinguishable from spine-like hairs).

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	0-1.0.0	0	0	1.0.0

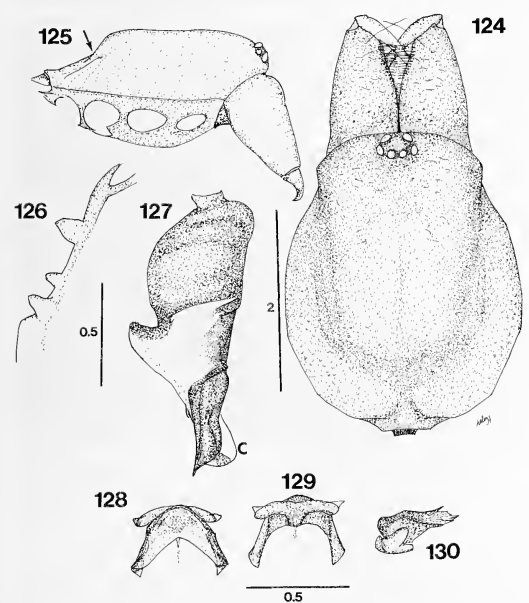
M. Knösel leg.; num. 37168; Stored at SMF Examined. New synonymy.
D. tabaibaensis Wunderlich 1991: 308, figs. 103–107 [♂]. Holotype male from Tabaiba, El Rosario, Tenerife, Canary Islands; 25 April 1990, C.G. Campos leg.; num. 03863; Stored at UL. Examined. New synonymy.
D. teideensis Wunderlich 1991: 309–310, figs. 112–118 [♂, ♀]. Holotype male from Retamar del Teide, La Orotava, Tenerife, Canary Islands; 21 April 1984, C.G. Campos leg.; num. 2772; Stored at UL. Examined. New synonymy.

Diagnosis.—*Dysdera macra* is distinguished from all other Canarian *Dysdera* species, except *D. brevisetae* and *D. esquiveli*, by a stepped carapace (Fig. 125) and spine-like hairs on legs. It differs from *D. esquiveli* by absence of eye reduction. It is distinguished from *D. brevisetae* in both sexes by possessing less granulation on chelicerae, shorter che-

liceral inner groove and distal and basal cheliceral teeth similar in size, and males by a barely visible lateral sheet (L) on the bulbus (Fig. 131).

Description.—*Neotype male*: Figs. 124–126, 131–134. Carapace (Fig. 124) 3.63 mm long; maximum width 2.93 mm; minimum width 2.1 mm. Dark red, uniformly distributed; slightly foveate at borders, wrinkled at middle, covered with a black, fine-textured, granular surface. Frontal border roughly round, about $\frac{3}{5}$ carapace length; anterior lateral borders slightly convergent; rounded at maximum dorsal width point, back lateral borders straight; back margin narrow, straight; stepped in lateral view (Fig. 125). AME diameter 0.16 mm; PLE 0.14 mm; PME 0.12 mm; AME on edge of frontal border, separated one from another about 1 diameter or more, close to PLE; PME very close to each other, about $\frac{2}{3}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; as long as wide at base (triangle-like); semi-circular groove at tip. Sternum dark red, uniformly distributed; slightly wrinkled; uniformly covered in slender black hairs.

Chelicerae (Fig. 126) 1.91 mm long, about $\frac{1}{3}$ of carapace length in dorsal view; fang medium-sized; 1.3 mm; basal segment smooth, with no granulations. Chelicera inner groove short, about $\frac{1}{3}$ cheliceral length; armed with three teeth and lamina at base; $D > B > M$ (large, D markedly larger); D trapezoid, located near segment tip; B close to basal lamina; M close to B. Legs dark orange-colored. Lengths of male described above: fe1 2.42 mm (all measurements in mm); pa1 1.63; ti1 2.19; me1 2; ta1 0.46; total 8.7; fe2 2.19; pa2 1.49; ti2 1.96; me2 1.86; ta2 0.42; total 7.92; fe3 1.77; pa3 1.11; ti3 1.21; me3 1.81; ta3 0.46; total 6.36; fe4 2.37; pa4 1.3; ti4 1.72; me4 2.23; ta4 0.56; total 8.18; relative length: $1 > 4 > 2 > 3$; palp: fe 1.68; pa 0.93; ti 0.74; ta 0.79; total 4.14. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal



Figures 124–130.—*Dysdera macra*. 124, Carapace, dorsal; 125, Carapace, lateral; 126, Left chelicera, ventral; 127, Right male bulb, external; 128, Vulva, dorsal; 129, Vulva, ventral; 130, Vulva, lateral. Scale bars in mm.

spines arranged in one band: distal 1.0.0; ti3 ventral 1 terminal spines. Fe4 dorsal spineless; ti4 dorsal spineless; ti4 ventral 1 terminal spines. Dorsal side of frontal legs smooth; ventral side of palp covered with a fine-textured, piligerous, granular surface; long, spine-like hairs on posterior ti, fe. Claws with 8 teeth or less, robust, length twice claw width.

Abdomen 4.19 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.027 mm long (small); medium thickness, roughly straight, not compressed, blunt, tip enlarged; uniformly, thickly distributed.

Male bulb (Fig. 127): T slightly smaller than DD; external distal border straight; internal sloped backwards. DD slightly bent in lateral view, clearly less than 45° ; internal distal border not expanded. ES more sclerotized than IS; IS truncated at DD middle part; ES bend markedly sclerotized. DD tip (Figs. 131–133) straight in lateral view. C present, short; distal end on DD internal tip; well-developed; located close to DD distal tip; proximal border sharply decreasing; distal border rounded, hardly stepped, upper tip not projected, rounded; external side hollowed. AC present. LF absent. L reduced to distal part; external end projected, pointed. AL present, very poorly developed; proximal border in posterior view fused with DH except for its most internal part. P (Fig. 134) fused to T; perpendicular to T in lateral view; lateral length about $\frac{1}{4}$ of T width; ridge present, perpendicular to T, not expanded; upper margin markedly toothed, on its distal part, few teeth (4–6); distally slightly projected; back margin not folded.

Female: (from Monte de Santa Ursula, S. Ursula, Tenerife; num. 3206, UB). Figs. 128–130, 135, 136. All characters as in male except: Carapace 3.4 mm long; maximum width 2.75 mm; minimum width 2.05 mm. AME diameter 0.16 mm; PLE 0.13 mm; PME 0.12 mm; PME $\frac{2}{5}$ diameter from PLE. Sternum dark orange, uniformly distributed; very slightly wrinkled, mainly between legs, frontal border.

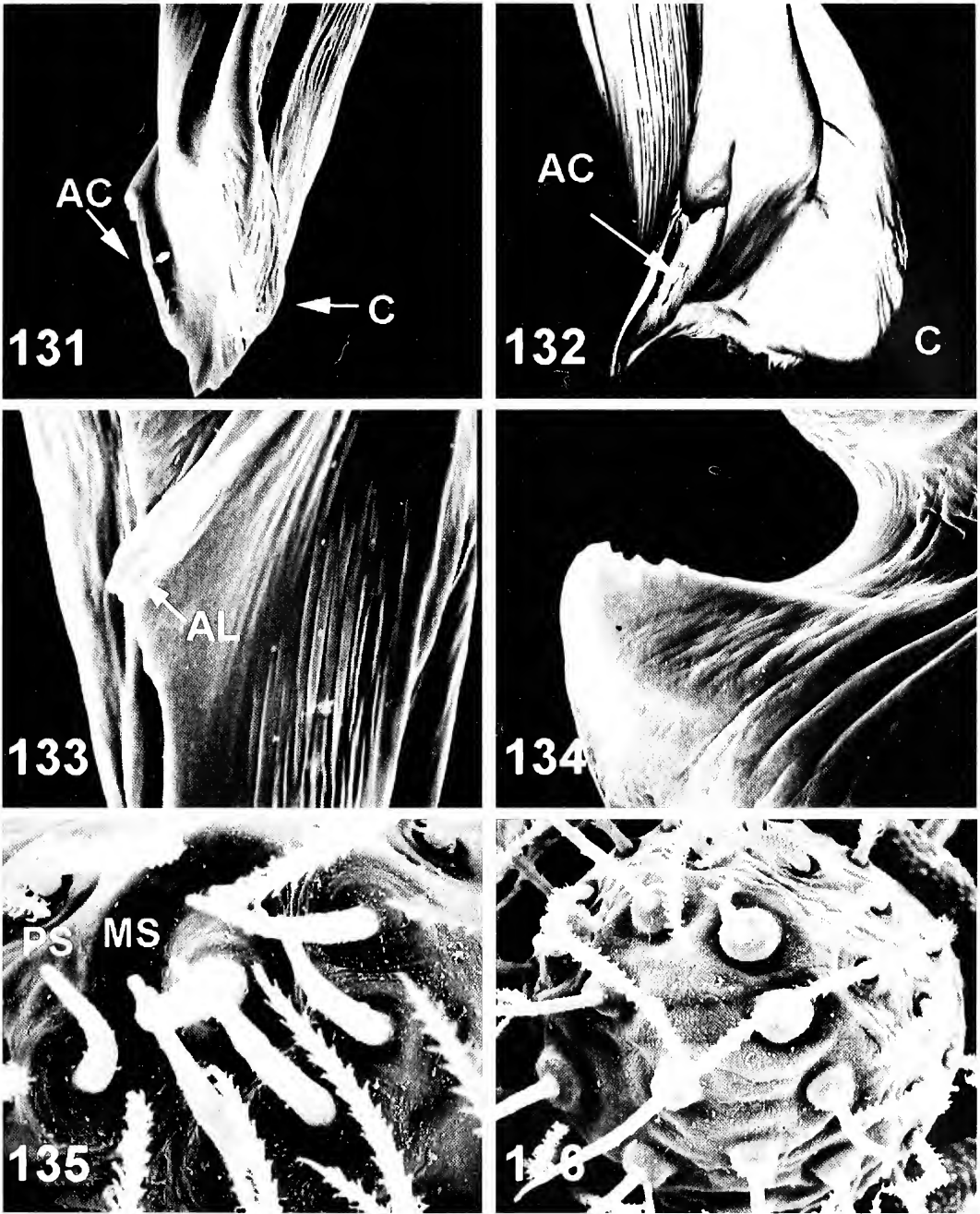
Chelicerae 1.86 mm long; fang 1.26 mm. Leg lengths of female described above: fe1 2.33 mm (all measurements in mm); pa1 1.54; ti1 1.96; me1 1.86; ta1 0.46; total 8.15; fe2 2.14; pa2 1.4; ti2 1.82; me2 1.77; ta2 0.42; total 7.55; fe3 1.77; pa3 1.02; ti3 1.21; me3

1.58; ta3 0.46; total 6.04; fe4 2.14; pa4 1.25; ti4 1.72; me4 1.96; ta4 0.51; total 7.58; relative length $1 > 4 > 2 > 3$; palp: fe 1.4; pa 0.7; ti 0.56; ta 0.74; total 3.4. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.0.0; distal 1.0.0-1; ti3 ventral 2 terminal spines. Fe4 dorsal spineless; ti4 dorsal spineless; ti4 ventral 2 terminal spines.

Abdomen 4.19 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.072–0.108 mm long; medium thickness, curved, compressed, blunt, tip enlarged; uniformly, thickly distributed. Vulva (Figs. 128–130) arch-like in dorsal view, frontally rounded; slightly wider than long; DF wide. MF poorly developed. VA frontal region completely sclerotized; posterior region sclerotized at anterior area. AVD hardly visible. S attachment not projected under VA; arms as long as DA, clearly curved; tips not projected; neck as wide as arms. TB usual shape. ALS (Figs. 135, 136) with PS; remaining piriform spigots more external than MS, arranged in one row; 4 + 1 piriform gland spigots; PMS, PLS with 5–10 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 2.75–3.63 mm, female from 2.93–3.45 mm. Carapace frontal lateral borders slightly convergent or parallel. AME separation from $\frac{2}{3}$ –1 diameter PLE-PME separation from $\frac{1}{3}$ – $\frac{2}{3}$ diameter. Sternum ornamentation variable, from smooth to slightly wrinkled. Chelicera relative length from $\frac{1}{3}$ – $\frac{2}{5}$. Basal segment lacking dorsal granulations, reduced to basal portion, or at distal internal margin. Chelicera inner groove from $\frac{1}{3}$ – $\frac{2}{5}$ its length. Fang relative size from $\frac{1}{3}$ – $\frac{2}{5}$. D only slightly larger than or as large as B. P relative size from $\frac{1}{4}$ – $\frac{2}{5}$. Female abdominal dorsal hair blunt, enlarged at frontal part and becoming pointed, longer to back. Spination variation given in Table 11.

Additional material examined.—**TENERIFE:** *Arafo:* 3 km N of Arafo, 950 m; 28 December 1994, 2♂ (F. Gasparo, FG). Fuente del Joco, 5 km NW of Arafo, 1930 m, 28 December 1994, 1♀ (F. Gasparo, FG). *Adeje:* Roque del Conde, 16 March 1996, 1♂ (Oromí, num. 3121 UB); 16 March 1996, 1♀ (Oromí, num. 3122 UB). *Arico:* Barranco del Rio, 14–21 April 1981, 1♂1♀, (J.M. Peraza, num. 2612 MCNT); 16–23 November 1984, 1♂ (J.M. Peraza, num. 2609 MCNT); 29 November 1993, 1♂ (M.A. Arnedo, num. 2576 UB). *El Rosario:* Ta-



Figures 131–136.—*Dysdera macra*, right male bulb and female spinnerets. 131, DD frontal; 132, DD external; 133, DD posterior; 134, P external; 135, Right ALS; 136, Right PLS.

baiba, MSS-2, 9 October 1990, 1 juv. (A.L. Medina, num. 2775 UL). *La Victoria de Acentejo*: El Diabillillo, 21 February 1997, 1 ♀, (P. Oromí, num. 3207 UB). Las Lagunetas, 28 January 1993, 1 ♂ (P. Oromí, num. 2547 UL); 27 March 1995, 1 ♀ (P. Oromí, num. 4110 UB). *Guía de Isora*: Above

Chío, 750 m, 28 December 1994, 2 ♂ 1 ♀, (F. Gasparo, FG). *Güímar*: Barranco del Agua, 14 January 1984, 1 ♀ (P. Oromí, num. 2681 UL); 17 January 1997, 1 ♀, (P. Oromí, num. 3194 UB). Barranco de Badajoz, 1900 m, 18 December 1996, 1 ♀ (P. Oromí, num. 3190 UB); 1800 m, 27 December

1996, 1 ♀ (P. Oromí, num. 3195 UB). *La Orotava*: Base del zig-zag, 17 October 1984, 2 ♀ (C.G. Campos, num. 2697 UL). Close to the Refugio, 2200 m, in VI, 1 ♂ 1 ♀ (C.G. Campos, num. 2627 SMF). Izaña, November 1994, 1 ♀, (Arnedo, num. 4827 (T40) UB). La Rosa de Piedra, 25 February 1996, 1 ♂, (Oromí & Emerson, num. 3126 UB). Las Cañadas del Teide, ?, 1 ♂ (A. Machado, num. 2808 UB); 17 May 1983, 1 ♀, (C.G. Campos, num. 2686 UL); 14 May 1993, 1 ♀ (P. Oromí, num. 2817 UB); 12 December 1993, 1 juv. (Oromí, num. 4837 (T52) UL); 3 June 1995, 1 ♂ (P. Oromí, num. 2969 UB); 11 June 1995, 1 ♀ (P. Oromí, num. 2968 UB); 24 May 1996, 1 ♀ (N. Zurita, num. 3173 UB). Teide, 2700m, 21 April 1984, 1 ♂ (C.G. Campos, num. 2766 UL). *Los Realejos*: La Fortaleza, 1 July 1990, 1 ♀ (C.G. Campos, num. 2760 UL). 17 May 1996, 1 juv. (N. Zurita, num. 3155 UB); 1 ♀ (A. Camacho, num. 3157 UB); 1 juv. (N. Zurita, num. 3158 UB); 1 ♀ (A. Camacho, 3156 UB). Roque Peral, 9 November 1983, 1 ♂ (C.G. Campos, num. 2701 UL); 19 April 1984, 1 ♂ (C.G. Campos, num. 2718 UL); 12 June 1984, 1 ♀ (C.G. Campos, num. 2693 UL); 18 June 1984, 2 ♂ (C.G. Campos, num. 2694 UL). *Santa Ursula*: Barranco del Pino, 15 November 1984, 1 ♀ (J.P. Peraza, num. 2737 UL). Monte de Santa Ursula, 13 December 1996, 3 ♂ 3 ♀ (P. Oromí, num. 3212 UB). *Vilaflor*: El Pinalito, 16–23 February 1985, 1 ♂ 1 ♀, (J.M. Peraza, num. 2610 MCNT); 24–31 May 1985, 1 ♂ (J.M. Peraza, num. 2611 MCNT). Madre del Agua, 15 March 1990, 1 ♂ (C.G. Campos, num. 2717 UL). *Dysdera teideensis*: **TENERIFE**: *La Orotava*: Retamar del Teide, 21 April 1984, 1 ♂ paratype (C.G. Campos, num. 2624 SMF). Las Cañadas del Teide, 18 October 1984, 1 ♀ paratype (C.G. Campos, num. 2719 UL). Teide, 3050 m, 21 April 1984, 1 ♂ paratype (C.G. Campos, num. 2703 UL).

Distribution.—Tenerifean endemic. A widespread species, collected throughout the island with the exception of Anaga and Teno massifs.

Comments.—The distribution of *D. macra* was unknown before the present study. Neither the original description (Simon 1883) nor the redescription of the species (Simon 1907) made any reference to its locality. Moreover, the report of this species in La Gomera by Strand (1911) has been claimed to be wrong (Arnedo et al. 1996).

The only type material of this species that was available for studying was a juvenile, probably the one originally described by Simon (1883) as the female of *D. macra*. However, in a subsequent article (Simon 1907) the same author transferred this specimen to *D.*

crocota. Fortunately, in this particular case both the original description and later redescription allowed the identification of the specimens belonging to this species. Arnedo et al. (1996) considered *D. macra* as a distinctive species on the basis of a double-toothed P. However, reexamination under SEM of some specimens formerly determined as *D. pergrada* and *D. teideensis* showed the presence of this character.

In their original descriptions (Wunderlich 1991), *D. pergrada*, *D. pseudopergrada*, *D. tabaibaensis* and *D. teideensis* were distinguished by: size of abdominal dorsal hairs, distal structures of the bulb and curvatures of P. In addition, *D. tabaibaensis* displayed a shorter distance between AME and relatively larger M tooth. Examination of the type material of these species, together with the study of about 40 newly available specimens, showed that (1) most of the formerly listed characters are polymorphic within the populations, (2) the suggested differences in the distal structures of the bulb simply do not exist and (3) the only truly distinguishable character, although present only in a single specimen, is the shorter AME distance of *D. tabaibaensis*, which seems to fit better that of *D. brevisetae*. However, both male genitalia and the remaining somatic characters of *D. tabaibaensis* correspond to those exhibited by the rest of the mentioned species. Finally, because all these species are compatible with the descriptions of *D. macra* and in order to avoid unnecessary proliferation of names, the preferred option has been to synonymize all these species with *D. macra*.

The *Dysdera teneriffensis* holotype seems to have been lost. Strand's original description is fully fitted by both *D. brevisetae* and *D. macra*. However, because the type locality (Aguamansa) is located into the distributional range of the second species, *D. teneriffensis* is better considered as a synonym of *D. macra*.

Dysdera minutissima Wunderlich 1991

Figs. 137–147, Table 12

Dysdera minutissima Wunderlich 1991: 299–300, fig. 61–62 [♂]. Holotype male from Aguamansa, La Orotava, Tenerife; 5 March 1987, H. Enghoff leg.; num. 2676; Stored at ZMK. Examined. - Wunderlich 1991: 284–287.

Diagnosis.—*Dysdera minutissima* is distinguished from most of the other Canarian *Dys-*

Table 12.—Intraspecific spination variability of *Dysdera minutissima*.

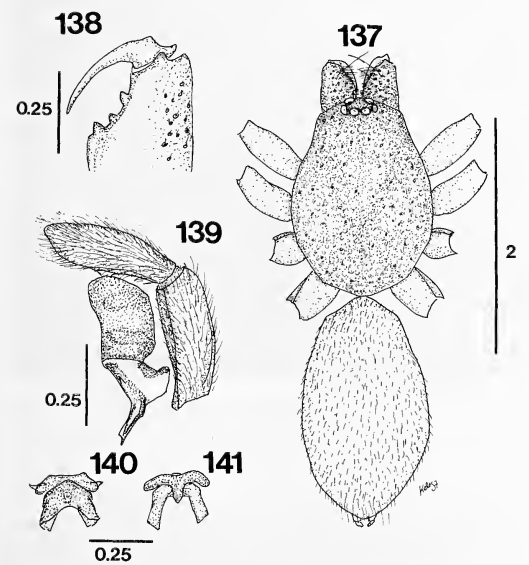
	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.0.0	0	0	1.0.0
Tibia 4 dorsal	0.0.0-1	0	0	0.0.0-1
Tibia 3 ventral	0	0	0	0
Tibia 4 ventral	0.0-1.0	0	0	0

dera species by its small size (carapace ~ 2.00 mm long) and markedly wrinkled carapace. In both sexes, it differs from the similar Tenerifean *D. levipes* and *D. gollumi* by having chelicerae with a granular surface, shorter cheliceral groove and spinated posterior legs. In males, the bulb distal division (DD) is longer than the tegulum (T) (Fig. 139) and the lateral sheet (L) has a distinct shape (Fig. 142). Males are distinguished from Grancanarian *D. andamanae* Arnedo & Ribera 1997 by absence of a lateral fold (LF) in bulb. In both sexes, it differs from *D. paucispinosa* Wunderlich 1991 from Gran Canaria and *D. orahan* Arnedo, Oromí & Ribera 1996 from La Gomera by possessing cheliceral granulation.

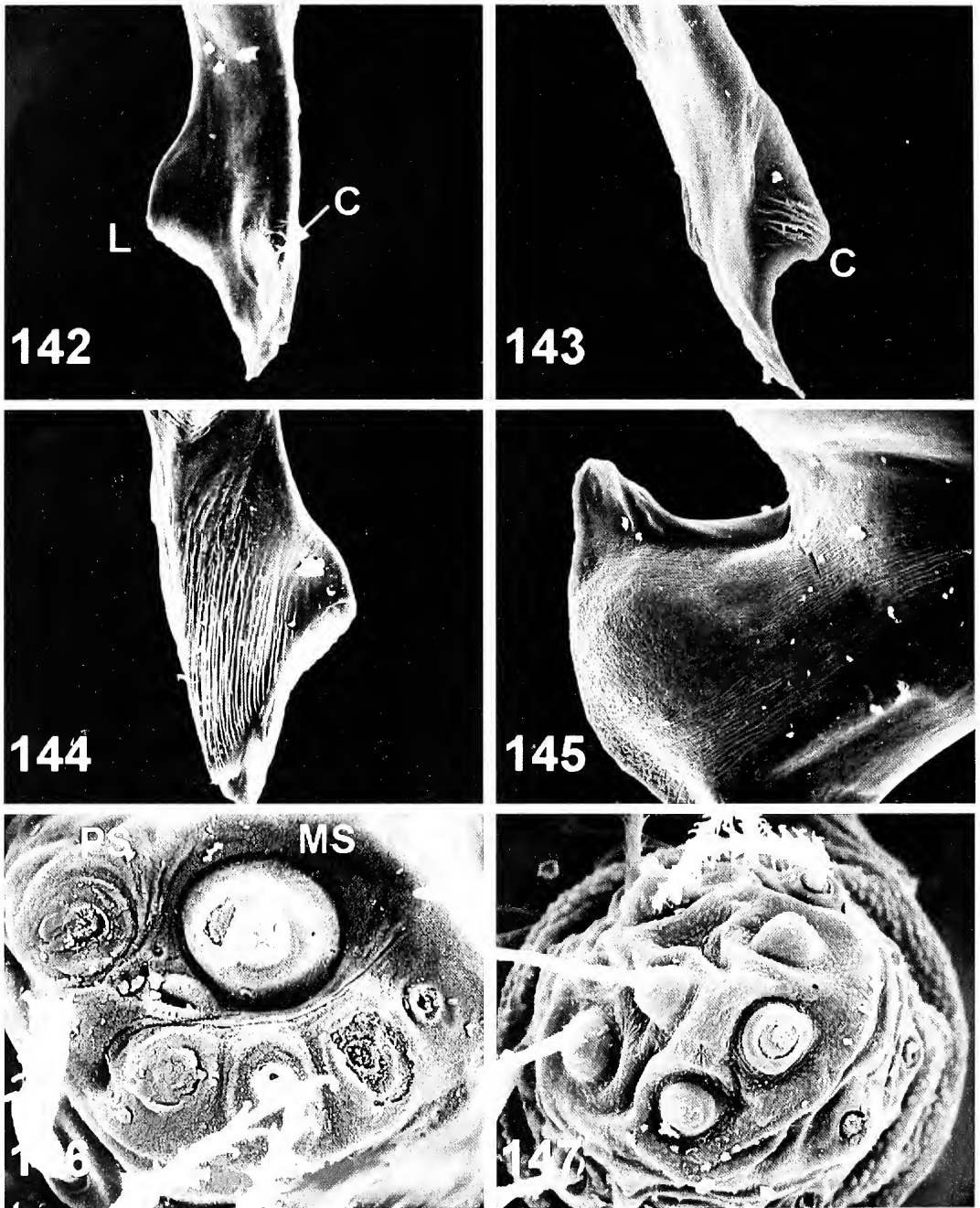
Description.—*Holotype male*: Figs. 137–139, 142–145. Carapace (Fig. 137) 1.49 mm long; maximum width 1.14 mm; minimum

width 0.74 mm. Dark red, darkened at borders; heavily wrinkled, foveate, covered with tiny granulations; hairy, covered with black hairs mainly at lateral and back borders. Frontal border roughly triangular, markedly smaller than ½ carapace length; anterior lateral borders divergent; rounded at maximum dorsal width point, back lateral borders straight; back margin narrow, straight. AME diameter 0.11 mm; PLE 0.09 mm; PME 0.09 mm; AME on edge of frontal border, separated one from another about ½ of diameter, close to PLE; PME very close to each other, about ⅓ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base (triangle-like); semicircular groove at tip. Sternum dark red, uniformly distributed; heavily wrinkled; uniformly covered in slender black hairs.

Chelicerae (Fig. 138) 0.53 mm long, about ¼ of carapace length in dorsal view; fang short, 0.32 mm; basal segment dorsal, ventral side completely covered with large piligerous granulations. Chelicera inner groove short, about ⅓ cheliceral length; armed with three teeth and lamina at base; D = M = B; D trapezoid, located roughly at center of groove; B close to basal lamina; M close to B. Legs pale yellow, darkened frontal, proximally. Lengths of male described above: fe1 1.26 mm (all measurements in mm); pa1 0.77; ti1 1.01; me1 0.97; ta1 0.35; total 4.36; fe2 1.13; pa2 0.77; ti2 0.9; me2 0.9; ta2 0.32; total 4.02; fe3 0.97; pa3 0.46; ti3 0.61; me3 0.83; ta3 0.3; total 3.17; fe4 1.22; pa4 0.63; ti4 0.99; me4 1.19; ta4 0.37; total 4.33; relative length: 1 = 4 > 2 > 3; palp: fe 0.79; pa 0.37; ti 0.39; ta 0.42; total 1.97. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.0.0; distal 1.0.0; ti3 ventral spines spineless; with two terminal spines. Fe4 dorsal spineless; ti4 dorsal spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4 ventral spines arranged



Figures 137–141.—*Dysdera minutissima*. 137, Carapace, dorsal; 138, Left chelicera, ventral; 139, Left male bulb, external; 140, Vulva, dorsal; 141, Vulva, ventral. Scale bars in mm.



Figures 142–147.—*Dysdera minutissima*, right male bulb and female spinnerets. 142, DD frontal; 143, DD external; 144, DD posterior; 145, P external; 146, Right ALS; 147, Right PLS.

in one band: proximal 0.0–1.0; with two terminal spines. Dorsal side of frontal legs covered with a fine-textured, piligerous, granular surface; ventral side of palp covered with hairs, lacking a granular surface. Claws with 10–14 teeth, slender, length twice claw width.

Abdomen 1.77 mm long; whitish; globular. Abdominal dorsal hairs 0.036–0.045 mm long; thin, curved (?), compressed (?), pointed (?), uniformly, thickly distributed.

Male bulb: (Fig. 139). T slightly longer than DD; external, internal distal border

Table 13.—Intraspecific spination variability of *Dysdera montanetensis*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.1-2.0-1	0.1-2.0-1	0	1.0.0-1
Tibia 4 dorsal	0-1.0-1.1	1.1-2.1	0	1.1-2.1
Tibia 3 ventral	1.2.0-1	0	0	1.0-1.0-1
Tibia 4 ventral	1.1.1	0-1.0-1.0-1	0.0-2.0-1	1.0-1.1
	Number of rows		Number of spines	
Femur 3 dorsal	1		0-1	
Femur 4 dorsal	1		1-4	

sloped backwards. DD bent about 45° in lateral view; internal distal border not expanded. ES wider, more sclerotized than IS; IS continuous to tip (?). DD tip (Figs. 142–144) straight in lateral view. C present, short; distal end on DD internal tip; well-developed; located far from DD distal tip; proximal border continuously decreasing; distal border sloping in its base, upper tip projected, rounded; external side smooth. AC absent. LF absent. L well-developed; external border not sclerotized, not folded; distal border divergent, continuous. AL absent. P (Fig. 145) fused to T; markedly sloped on its proximal part, perpendicular on distal; lateral length from ½–⅔ of T width; ridge present, perpendicular to T, not expanded; upper margin markedly toothed, on its distal part, very few teeth (1–3); not distally projected; back margin not folded.

Female: (from Barranco del Pino, Santa Ursula, Tenerife; num. 2614, MCNT), Figs. 140–141, 146, 147. All characters as in male except: Carapace 1.68 mm long; maximum width 1.26 mm; minimum width 0.74 mm. Dark brownish-red. AME diameter 0.11 mm; PLE 0.09 mm; PME 0.08 mm; AME separated one from another about ⅔ of diameter. Sternum brownish-red; heavily wrinkled.

Chelicerae 0.53 mm long; fang 0.37 mm. Leg lengths of female described above: fe1 1.24 mm (all measurements in mm); pa1 0.7; ti1 1.04; me1 0.99; ta1 0.35; total 4.32; fe2 1.15; pa2 0.77; ti2 0.9; me2 95; ta2 0.32; total 4.09; fe3 1.01; pa3 0.51; ti3 0.65; me3 0.86; ta3 0.3; total 3.33; fe4 1.35; pa4 0.65; ti4 1.08; me4 1.28; ta4 0.37; total 4.73; relative length 4 > 1 > 2 > 3; palp: fe 0.65; pa 0.37; ti 0.37; ta 0.48; total 1.87. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.0.0; distal 1.0.0; ti3 ventral spines spineless; with

one terminal spine on anterior margin. Fe4 dorsal spineless; ti4 dorsal spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4 ventral spines arranged in one band: proximal 0.1-0.0; with two terminal spines.

Abdomen 1.96 mm long; whitish; globular. Abdominal dorsal hairs 0.054–0.063 mm long; thin, curved, compressed, pointed; uniformly, thickly distributed. Vulva (Figs. 140, 141) arch-like in dorsal view, frontally pointed; as wide as long; DF wide. VA frontal region completely sclerotized. S attachment projected under VA; arms as long as DA, clearly curved; tips dorsally projected; neck as wide as arms. TB usual shape. ALS (Figs. 146, 147) with PS; remaining piriform spigots more external than MS, arranged in one row; 4 + 1 piriform gland spigots; PMS, PLS with 5–10 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 1.49–1.54 mm. AME separation from ½–⅔ diameter. PLE-PME from ⅓–⅔ diameter apart. Cheliceral teeth very similar in size. D > B > M. Spination variability in Table 12.

Additional material examined.—**TENERIFE:** *Santa Ursula*: Barranco del Pino, 21–28 July 1985, 1♂ (J.M. Peraza, num. 2615 MCNT).

Distribution.—Tenerifean endemic. Known from two localities on middle-northern slope of the island.

Comments.—Female specimens of this species were formerly unknown. Unfortunately, during manipulation of the only available vulva it was lost. The character states reported for the vulva in the present work are based on preliminary drawings made before its loss.

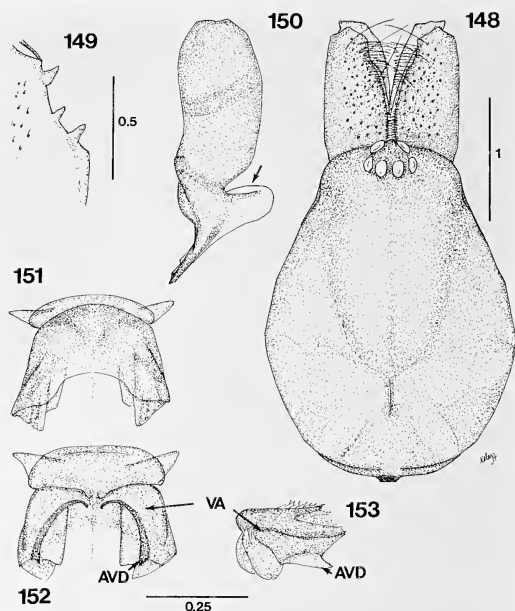
Dysdera montanetensis Wunderlich 1991
Figs. 148–159, Table 13
Dysdera montanetensis Wunderlich 1991: 300–301,
fig. 63–64 [♂]. Holotype male from La Monta-

ñeta, MSS 6–9, Garachico, Tenerife; 26 April 1988, A.L. Medina leg.; num. T-64-17; Stored at UL. Examined. -Wunderlich 1991: 284–287.

Diagnosis.—*Dysdera montanetensis* males are distinguished from most other Canarian species by a distinctly expanded, unsclerotized upper margin of posterior apophysis (P) (also present in *D. gibbifera* and *D. volcania*) (Fig. 150) in the male bulb. Females are distinguishable by the presence of ridges on vulva ventral arch (VA) (Figs. 152, 153) (also present in *D. labradaensis* and *D. iguanensis*). *Dysdera montanetensis* differs from *D. gibbifera* by its smaller size, markedly spinated legs and, in males, by lack of lateral sheet (L) sclerotization (Fig. 155). Males and females are distinguished from *D. volcania* by possessing smooth carapace and markedly spinated legs, from *D. iguanensis* by more distal location of cheliceral distal tooth (Fig. 149) and distinct spination pattern (Table 13) and from *D. labradaensis* by smaller size and lack of eye reduction.

Description.—*Holotype male*: Figs. 148–150, 154–157. Carapace (Fig. 148) 2.98 mm long; maximum width 2.35 mm; minimum width 1.37 mm. Brownish-orange, uniformly distributed; slightly foveate at borders, wrinkled at middle, covered with tiny granulations. Frontal border roughly round, markedly smaller than $\frac{1}{2}$ carapace length; anterior lateral borders slightly divergent or parallel; rounded at maximum dorsal width point, back lateral borders straight; back margin wide, straight. AME diameter 0.18 mm; PLE 0.18 mm; PME 0.12 mm; AME on edge of frontal border, separated one from another about $\frac{1}{2}$ diameter, close to PLE; PME very close to each other, about $\frac{1}{3}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base (rectangle-like); semicircular groove at tip. Sternum brownish-orange, frontally darker, becoming lighter towards back; wrinkled; covered in hairs mainly on margin.

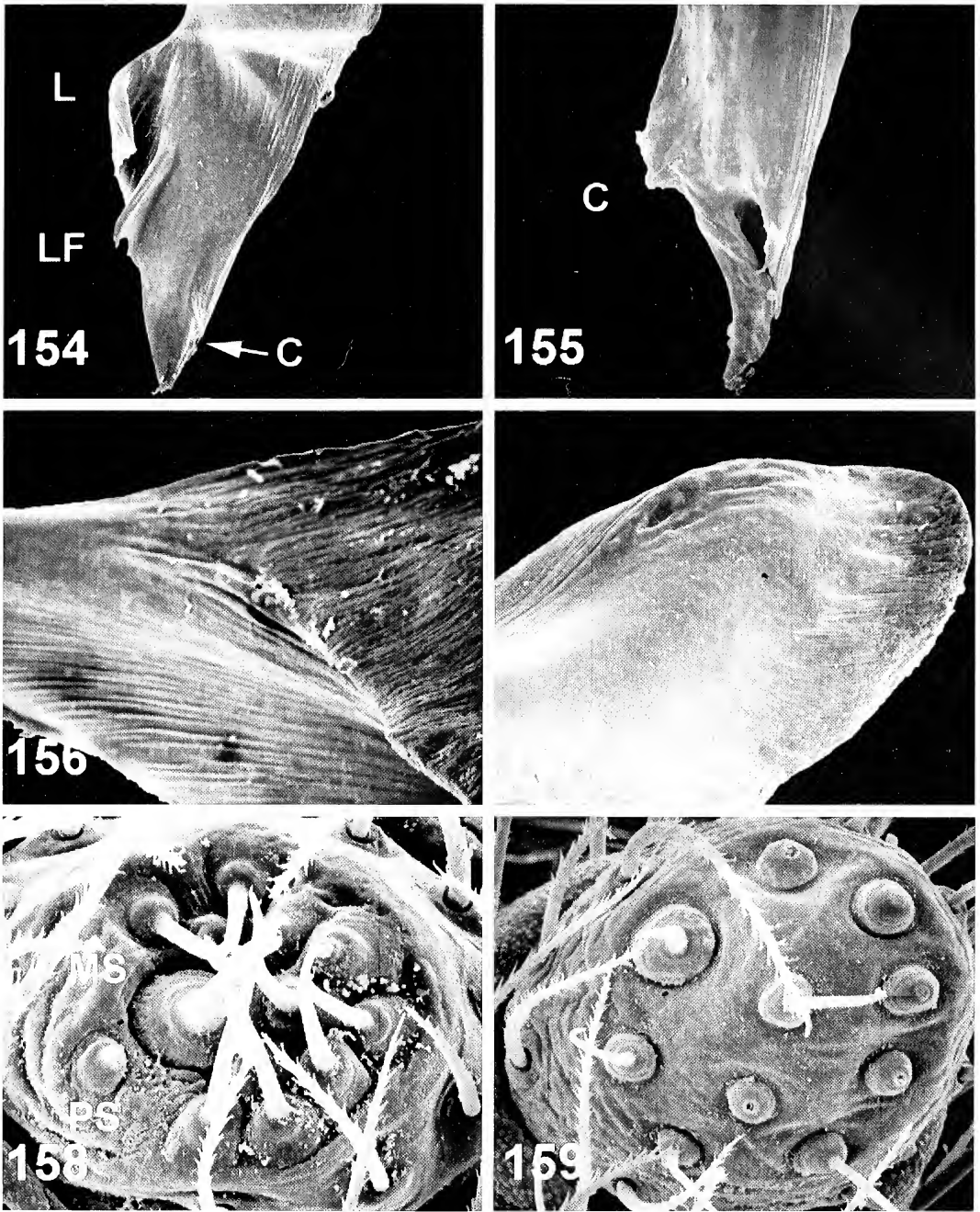
Chelicerae (Fig. 149) 1.21 mm long, about $\frac{1}{3}$ of carapace length in dorsal view; fang short, 0.84 mm; basal segment dorsal, ventral side completely covered with large piligerous granulations. Chelicera inner groove short, about $\frac{1}{3}$ cheliceral length; armed with three teeth and lamina at base; $D > B > M$ (large, not very different); D trapezoid, located near segment



Figures 148–153.—*Dysdera montanetensis*. 148, Carapace, dorsal; 149, Right chelicera, ventral; 150, Right male bulb, internal; 151, Vulva, dorsal; 152, Vulva, ventral; 153, Vulva, lateral. Scale bars in mm.

tip; B close to basal lamina; M at middle of B and D. Legs yellow, frontal slightly darker. Lengths of male described above: fe1 2.75 mm (all measurements in mm); pa1 1.72; ti1 2.42; me1 2.47; ta1 0.74; total 10.1; fe2 2.7; pa2 1.63; ti2 2.28; me2 2.42; ta2 0.74; total 9.77; fe3 2.28; pa3 1.21; ti3 1.64; me3 2.16; ta3 0.7; total 7.98; fe4 3.17; pa4 1.54; ti4 2.47; me4 3.17; ta4 0.79; total 11.09; relative length: $4 > 1 > 2 > 3$; palp: fe 1.35; pa 0.74; ti 0.93; ta 0.84; total 3.86. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spines in one row: 1; ti3 dorsal spines arranged in three bands: proximal 1.1.1; medial-proximal 0.2.0-1; distal 1.0.0-1; ti3 ventral spines arranged in two bands: proximal 1.2.1-0; distal 1.0.0-1; with two terminal spines. Fe4 dorsal spines in one row: 2-3; ti4 dorsal spines arranged in three bands: proximal 0-1.1.1; medial-proximal 1.1-2.1; distal 1.2.1; ti4 ventral spines arranged in four bands: proximal 1.1.1; medial-proximal 1-0.1.0; medial-distal 0.1.0; distal 1.1.1; with two terminal spines. Dorsal side of frontal legs, ventral side of palp with a fine-textured, piligerous, granular surface. Claws with more than 15 teeth, slender, length twice claw width.

Abdomen 3.03 mm long; whitish; cylindri-



Figures 154–159.—*Dysdera montanetensis*, right male bulb and female spinnerets. 154, DD frontal; 155, DD internal; 156, DD posterior; 157, P internal; 158, Right ALS; 159, Right PLS.

cal. Abdominal dorsal hairs 0.072 mm long; thick, slightly curved, not compressed, blunt, tip not enlarged; uniformly, scanty distributed.

Male bulb (Fig. 150): T slightly longer than DD; external, internal distal border sloped

backwards. DD bent about 45° in lateral view; internal distal border not expanded. IS and ES equally developed; IS continuous to tip (?). DD tip (Figs. 154–156) straight in lateral view. C present, short; distal end on DD internal tip; poorly developed; located far from

DD distal tip; proximal border continuously decreasing; distal border sloping in its base, upper tip not projected, pointed; external side hollowed. AC absent. LF present; distally projected; well-developed. L well-developed; external border not sclerotized, laterally markedly folded; distal border divergent, continuous. AL absent. P (Fig. 157) fused to T; markedly sloped on its proximal part, perpendicular on distal; lateral length as long as or longer than T width; ridge present, not sclerotized, perpendicular to T, distinctly expanded, rounded; upper margin smooth; not distally projected; back margin not folded.

Female: (from Cueva Labrada, El Sauzal, Tenerife; num. 2519, UL; Figs. 151–153, 158, 159.) All characters as in male except: Carapace 3.35 mm long; maximum width 2.57 mm; minimum width 1.58 mm. Anterior lateral borders divergent. AME diameter 0.21 mm; PLE 0.2 mm; PME 0.14 mm.

Chelicerae 1.35 mm long, fang 0.93 mm. Leg lengths of female described above: fe1 2.93 mm (all measurements in mm); pa1 1.91; ti1 2.56; me1 2.56; ta1 0.74; total 10.7; fe2 2.89; pa2 1.77; ti2 2.42; me2 2.56; ta2 0.79; total 10.43; fe3 2.28; pa3 1.4; ti3 2.16; me3 2.33; ta3 0.79; total 8.89; fe4 3.54; pa4 1.77; ti4 2.76; me4 3.54; ta4 0.98; total 12.59; relative length $4 > 1 > 2 > 3$; palp: fe 1.54; pa 0.84; ti 0.74; ta 1.16; total 4.28. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spines in one row: 1; ti3 dorsal spines arranged in three bands: proximal 1.1.1-0; medial-proximal 0.1-2.0-1; distal 1.0.0-1; ti3 ventral spines arranged in two bands: proximal 1.2.0; distal 1.0-1.1-0; with two terminal spines. Fe4 dorsal spines in one row: 1-3; ti4 dorsal spines arranged in three bands: proximal 0-1.0.1; medial-proximal 1.2.1; distal 1.2.1; ti4 ventral spines arranged in three bands: proximal 1.1.1; medial-proximal 0; medial-distal 0.1-2.0; distal 1.0.1; with two terminal spines.

Abdomen 6.52 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.09 mm long; medium thickness, slightly curved, not compressed, blunt, tip not enlarged; uniformly, scantily distributed. Vulva (Figs. 151–153) rectangle-like in dorsal view, frontally rounded; slightly wider than long; DF wide. MF well-developed; sclerotized along its extent. VA frontal region completely sclerotized; posterior region sclerotized except for most internal area; sclerotized ridge at ventral VA ex-

ternal margin, as long as VA. AVD clearly recognizable. S attachment projected under VA; arms as long as DA, straight; tips dorsally projected; neck as wide as arms. TB usual shape. ALS (Figs. 158, 159) with PS; remaining piriform spigots no more external than MS, arranged in three rows; $10 + 1$ piriform gland spigots; PMS, PLS with 5–10 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 2.98–3.07 mm., female from 2.93–4.00 mm. AME separation from $\frac{1}{2}$ – $\frac{2}{3}$ of diameter. PLE-PME from $\frac{1}{3}$ – $\frac{1}{2}$ diameter apart. D markedly larger than or as large as B. Usually, teeth large, not markedly different. In some females (Teno, Labrada) abdomen hairs are compressed and pointed. Vulva as wide as long. Labrada female specimen #2516 shows carapace frontal lateral margins parallel, long. Carapace, sternum ornamentation nearly smooth. Strong reduction in eye size. D at center of the chelicera groove. Reduction in leg pigmentation, spination: absence of fe spination and ti medial spination. Spination variation given in Table 13.

Additional material examined.—**TENERIFE:** *El Rosario:* Las Raíces, ? November 1993, 1 ♀ (Arnedo & Ribera, num. 4795 UB). *La Orotava:* Aguamansa, MSS, 4 August 1985, 1 ♂ (J.L. Martín & A. Machado, num. 2580 UL). *El Sauzal:* Cueva Labrada, 4 November 1991, 1 ♀, (J.L. Martín, num. 2516 UB). *Los Silos:* Monte del Agua, 24 February 1997, 1 ♀ (N. Zurita, num. 3209 UB). *Vilaflor:* Fuente de Mesa, 9 March 1984, 1 ♀ (J.M. Peraza, num. 2770 UL).

Distribution.—Tenerifean endemic. Known from several localities spread throughout the northern slope excepting Anaga massif, and from a single locality at middle-southern slope.

Comments.—Former knowledge of this species was restricted to a single male specimen.

Dysdera propinqua Ribera, Ferrández & Blasco 1985

Figs. 160–172, Table 14

Dysdera propinqua Ribera, Ferrández & Blasco 1985: 61–63, fig. 4A–D [♂]. Holotype male from Cueva Honda, Güímar, Tenerife; 15 December 1982, J.L. Martín leg.; num. T-CH-14; Stored at UL. Examined. -Wunderlich 1991: 284–287. Examined.

D. nesioties: Simon 1907: 260 (♀, non ♂). Simon

Table 14.—Intraspecific spination variability of *Dysdera propinqua*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.0-1.0-1	0	0	1.0.0
Tibia 4 dorsal	0-1.0.1	0	0	0.0.1
Tibia 3 ventral	0.0-1.0	0	0	0
Tibia 4 ventral	0.0-1.0	0	0	0
	Number of rows		Number of spines	
Femur 3 dorsal	0		0	
Femur 4 dorsal	2		0-1/1-4	

1883: 297 (*D. insulana* ♀, non ♂) 3 type females, unknown locality, Canary Islands; unknown data, M. Verneau leg.; num. B-536; Stored at MNHN. Examined. Incorrect identification.

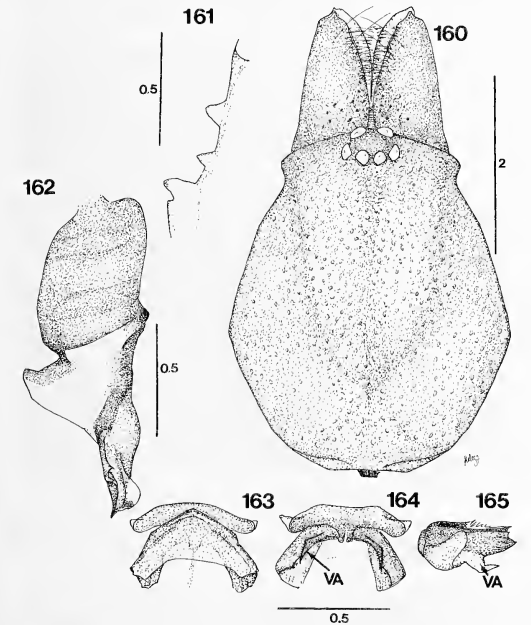
D. obscuripes Wunderlich 1991: 302–303, figs. 72–76 [♂, ♀]. Holotype male from pine forest close to La Orotava, La Orotava, Tenerife, Canary Islands; in Il., M. Knösel leg.; Stored at SMF. Holotype not examined, paratypes examined. New synonymy.

Diagnosis.—*Dysdera propinqua* is distinguished, in both sexes, from most other Canarian species by a combination of markedly

foveate carapace, convergent anterior lateral carapace borders and poorly spinated posterior legs. Males and females differ from the similar and sympatric *D. cribellata*, by the basal cheliceral teeth not being the largest and presence of cheliceral granulation. *Dysdera propinqua* males differ from *D. cribellata* by lacking a fold in the lateral sheet (L) of the bulb, and in females by presence of tooth-shaped expansions in the vulval ventral arch (VA) (Figs. 164, 165).

Description.—*Holotype male*: Figs. 160–162, 166–170. Carapace (Fig. 160) 4.1 mm long; maximum width 3.4 mm; minimum width 2.17 mm. Dark red, darkened at borders; foveate at borders, slightly wrinkled at middle, with a black, fine-textured, granular surface; hairy, covered with black hairs mainly at lateral and back borders. Frontal border roughly triangular, from ½–⅔ carapace length; anterior lateral borders convergent; rounded at maximum dorsal width point, back lateral borders straight; back margin wide, straight. AME diameter 0.27 mm; PLE 0.25 mm; PME 0.18 mm; AME on edge of frontal border, separated one from another about ⅔ of diameter, close to PLE; PME very close to each other, about ⅓ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base (triangle-like); semi-circular groove at tip. Sternum dark red, darkened on borders; mostly wrinkled, except in middle part; uniformly covered in slender black hairs.

Chelicerae (Fig. 161) 2.1 mm long, about ⅔ of carapace length in dorsal view; fang medium-sized, 1.47 mm; basal segment dorsal side completely covered with piligerous granulations, ventral side smooth (spacing distally reduced). Chelicera inner groove short, about



Figures 160–165.—*Dysdera propinqua*. 160, Carapace, dorsal; 161, Left chelicera, ventral; 162, Right male bulb, external; 163, Vulva, dorsal; 164, Vulva, ventral; 165, Vulva, lateral. Scale bars in mm.

$\frac{1}{2}$ cheliceral length; armed with three teeth and lamina at base; $D = B > M$; D round, located roughly at center of groove; B close to basal lamina; M close to B. Legs orange. Lengths of male described above: fe1 3.92 mm (all measurements in mm); pa1 2.65; ti1 3.54; me1 3.41; ta1 0.76; total 14.28; fe2 3.36; pa2 2.4; ti2 2.96; me2 3.16; ta2 0.76; total 12.64; fe3 2.6; pa3 1.49; ti3 1.89; me3 2.4; ta3 0.58; total 8.96; fe4 3.46; pa4 1.89; ti4 2.76; me4 3.21; ta4 0.83; total 12.15; relative length: $1 > 2 > 4 > 3$; palp: fe 1.25; pa 1.06; ti 1.14; ta 1.08; total 4.53. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.0.1; distal 1.0.0-1; ti3 ventral 2 terminal spines. Fe4 dorsal spines in two rows: anterior 1-0; posterior 4-3; ti4 dorsal spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4 ventral 2 terminal spines. Dorsal side of frontal legs with a piligerous, fine-textured, granular surface; ventral side of palp covered with hairs, without a granular surface; very long hairs on back legs as well as on palps. Claws with 8 teeth or less, robust, hardly larger than claw width.

Abdomen 6.02 mm long; cream-colored; cylindrical. Abdominal dorsal hairs 0.144 mm long; thick, roughly straight, compressed, lanceolate, frontally curved; uniformly, thickly distributed.

Male bulb (Fig. 162): T slightly smaller than DD; external, internal distal border sloped backwards. DD slightly bent in lateral view, clearly less than 45° ; internal distal border not expanded. IS and ES equally developed; IS truncated at DD middle part. DD tip (Figs. 166-169) straight in lateral view. C present, short; distal end on DD internal tip; well-developed; located close to DD distal tip; proximal border sharply decreasing; distal border stepped, upper tip not projected, rounded; external side hollowed. L well-developed; external border not sclerotized, distally markedly folded; distal border divergent, discontinuous but without a fold at the middle. AL present, hardly visible except for a small notch; proximal border in posterior view fused with DH except for its most internal part. P (Fig. 170) fused to T; perpendicular to T in lateral view; lateral length from $\frac{2}{5}$ - $\frac{1}{2}$ of T width; ridge present, perpendicular to T, not expanded; upper margin markedly toothed, along its

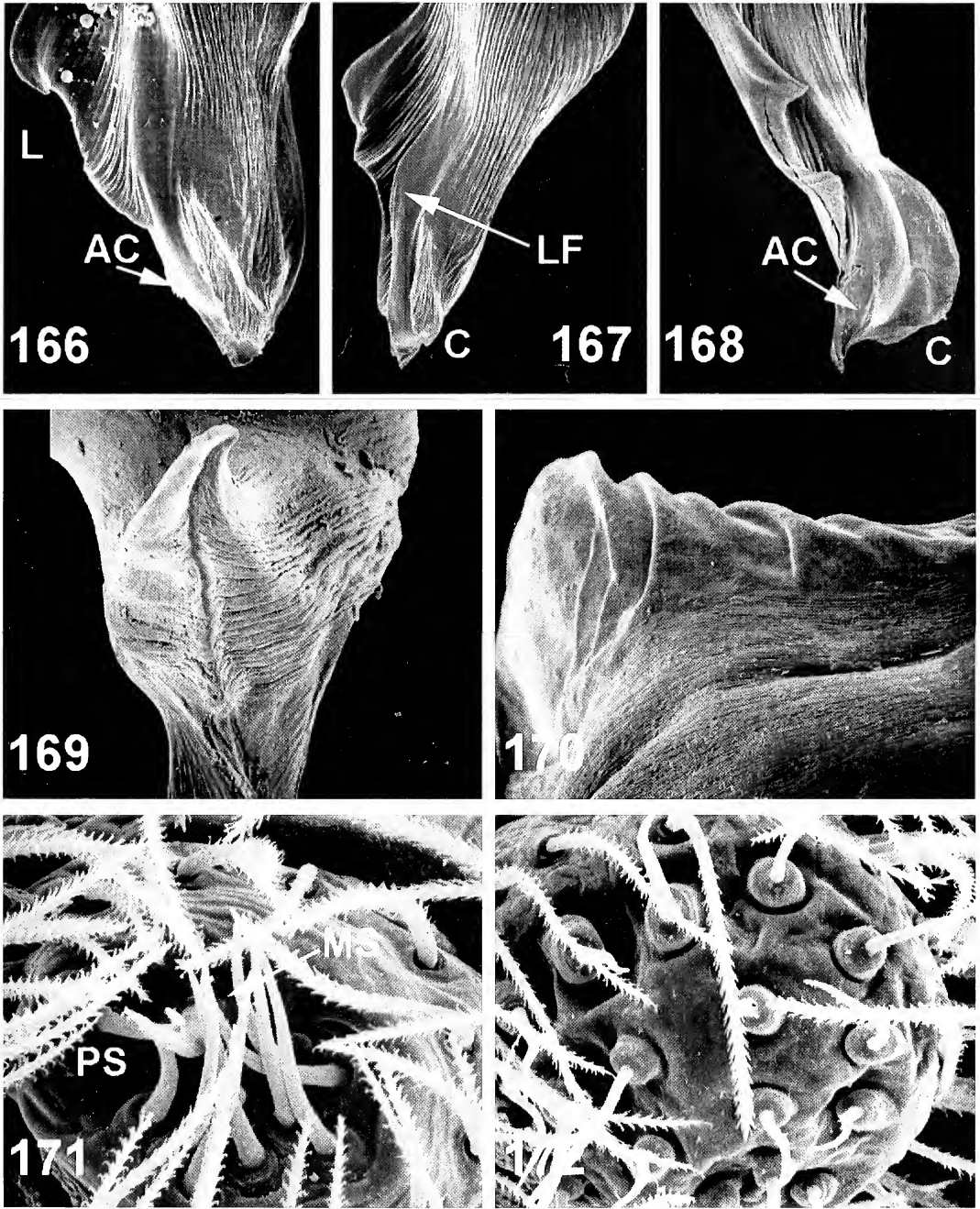
extent, few teeth; not distally projected; back margin not folded.

Female: (from Barranco de Badajoz, Güímar, Tenerife; num. 3192, UB; Figs. 163-165, 171, 172.) All characters as in male except: Carapace 4.34 mm long; maximum width 3.57 mm; minimum width 2.52 mm. AME diameter 0.23 mm; PLE 0.21 mm; PME 0.16 mm; PME $\frac{2}{5}$ diameter from PLE. Sternum brownish-red.

Chelicerae 2.03 mm long; fang 1.33 mm. Leg lengths of female described above: fel 3.43 mm (all measurements in mm); pa1 2.31; ti1 2.87; me1 2.87; ta1 0.66; total 12.14; fe2 3.22; pa2 2.17; ti2 2.52; me2 2.73; ta2 0.63; total 11.27; fe3 2.45; pa3 1.47; ti3 1.82; me3 2.31; ta3 0.63; total 8.68; fe4 3.57; pa4 1.89; ti4 2.73; me4 2.15; ta4 0.77; total 12.11; relative length $1 > 4 > 2 > 3$; palp: fe 2.03; pa 1.05; ti 0.84; ta 1.12; total 5.04. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.1-0.1; distal 1.0.0; ti3 ventral 2 terminal spines. Fe4 dorsal spines in two rows: anterior 1; posterior 3; ti4 dorsal spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4 ventral 2 terminal spines.

Abdomen 6.23 mm long; cream-colored; cylindrical. Abdominal dorsal hairs 0.153 mm long; thick, roughly straight, compressed, lanceolate, frontally curved; uniformly, thickly distributed. Vulva (Figs. 163-165) arch-like in dorsal view, frontally pointed; slightly wider than long; DF wide. MF poorly developed. VA frontal region completely sclerotized; posterior region sclerotized at anterior area; tooth-shaped expansion from internal back border, not joined to lateral sclerotization, slightly shorter than DF lateral margins, markedly bent towards lateral area. AVD hardly visible. S attachment not projected under VA; arms as long as DA, clearly curved; tips dorsally projected; neck as wide as arms. TB usual shape. ALS (Figs. 171-172) with PS; remaining piriform spigots more external than MS, arranged in three rows; $9 + 1$ piriform gland spigots; PMS, PLS with 10-15 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 3.54-4.43 mm, female from 3.77-4.69 mm. Sternum ornamentation variable, from hardly wrinkled between coxae to completely wrinkled. Chelicera lacking dorsal distal granulations or



Figures 166–172.—*Dysdera propinqua*, right male bulb and female spinnerets. 166, DD frontal, LF absent; 167, DD, frontal, LF present; 168, DD external; 169, DD posterior; 170, P external; 171, Right ALS; 172, Right PLS.

somewhat reduced. P $\frac{1}{3}$ of T width. One specimen from Teno with well-developed LF (Fig. 167). Vulva frontally round. Ventral tooth-shaped sclerotization shorter, about $\frac{1}{3}$ of DF lateral length. Spination variation given in Table 14.

Additional material examined.—**TENERIFE:** ? : ?; 24 February 1984, 1♂ (N.P. Ashmole, num. 2728 UL). Fuente de Mesa, 9 March 1984, 2♀ (J.M. Peraza, num. 2770 UL). *Adeje:* Roque del Conde, 16 March 1996, 1♂ (Oromí, num. 3123 UB); 1♀ (Oromí, num. 3124 UB). *Arafo:* Fuente

del Joco, 5km NW from Arafo, 1930 m, 28 December 1994, 2♀ (F. Gasparo, FG). *Arico*: Barranco del Rio, 22 February 1984, 1juv. (P. Ashmole, num. 2685 UL); 15–22 October 1984, 1♂ (J.M. Peraza, num. 2772 UL); 16–23 November 1984, 1♂1♀ (J.M. Peraza, num. 2721 UL); 17–26 September 1985, 1♂1♀ (J.M. Peraza, num. 2613 MCNT). *Buenavista*: Barranco de las Cuevas, 4 February 1989, 1♀ (H. Enghoff, num. 2642 ZMK). Casa Blanca close to W Buenavista, 4 February 1989, 1♀ (H. Enghoff, num. 2650 ZMK). *El Rosario*: Las Raices, November 1993, 1♂ (Arnedo & Ribera, num. 4796 (T17) UB). *Granadilla*: Madre del Agua, November 1993, 1♀ (Arnedo & Fluhr, num. 4797 (T22) UB); 1juv. (Arnedo & Fluhr, num. 4798 (T42) UB); 1♂ (Arnedo & Fluhr, num. 4813 (T4) UB). *Gülfar*: Barranco de Badajoz, 18 December 1996, 4♀, (P. Oromí, num. 3210 UB). *La Laguna*: Bajamar, 10 September 1985, 1♂ (J.M. Peraza, num. AR-202 MCNT). El Moquinal, 23 January 1997, 1♂3♀ (P. Oromí, num. 3196 UB). Monte de las Mercedes, 18 March 1990, 1♂ (C.G. Campos, num. 2726 UL). *La Orotava*: Base zig-zag, 17 October 1984, 1♂ (C.G. Campos, num. 2696 UL). El Guanche close to Aguamansa, 5 March 1987, 1♂ (H. Enghoff, num. 2649 ZMK). Hierba Pajonera, 2050 m, 19 June 1984, 1♂ (C.G. Campos, num. 2724 UL). Izaña, 13 March 1987, 1♀ (H. Enghoff, num. 2641 ZMK). Las Cañadas del Teide, 1♀, (J. Wunderlich, num. 2629 JW); 1 March 1984, 1♂ (C.G. Campos, num. 2761 UL); 19 April 1984, 1♂ (C.G. Campos, num. 2763 UL); 2100 m, 18 June 1984, 1♀ (C.G. Campos, num. 2725 UL); 19 September 1984, 1♀ (C.G. Campos, num. 2762 UL); 2050 m, 10 November 1984, 1♀, (C.G. Campos, num. 2722 UL); 29 June 1995, 1juv. (A. Camacho, num. 3159 UB); 2 May 1996, 1♂ (N. Zurita, num. 3171 UB). Montaña de Los Conejos, 2400 m, 18 June 1984, 1♂ (C.G. Campos, num. 2723 UL). Pico Viejo, 9 November 1983, 1♀ (C.G. Campos, num. 2695 UL). Retamar, 3050 m, 19 June 1984, 1juv. (C.G. Campos, num. 2765 UL). Teide, 2700 m, 19 June 1984, 1♂1♀ (C.G. Campos, num. 2713 UL). 3050 m, 18 September 1984, 1juv. (C.G. Campos, num. 2764 UL). Ucanca, 2100 m, 1 July 1990, 1♂ (C.G. Campos, num. 2745 UL). *Santa Cruz de Tenerife*: Bailadero, November 1993, 1♂ (Arnedo & Ribera, num. 4833 (T47) UB). Anaga, Cruz del Carmen, 12 May 1996, 1♂1♀ (M. Naranjo, num. 3146 UB); 1♀ (M. Naranjo, num. 3147 UB). Taganana, 1♂ (Oromí, num. 2932 UB). *Los Realejos*: La Fortaleza, 25 February 1983, 1♂ (A. Fox, num. 2727 UL); 26 December 1984, 1♂ (C.G. Campos, num. 2699 UL). Pinar Roque Peral, 19 May 1984, 1♂ (C.G. Campos, num. 2692 UL); 18 October 1984, 1♂ (C.G. Campos, num. 2698 UL); 1♂, 1juv. (C.G. Campos, num. 2700 UL). *Los Silos*: Teno, Monte del Agua, 1 February 1988, 1♂1♀ (J.J. Naranjo, num. 2598 UL); 1♂2♀ (P. Oromí, num. 2683

UL); 1 March 1989, 2♀ (P. Oromí, num. 2684 UL); 30 November 1993, 1♂ (M.A. Arnedo, num. 3181 UB). *Santa Ursula*: Barranco del Pino, 15 November 1984, 4♀ (J.M. Peraza, num. 2720 UL). Monte de Santa Ursula, 13 December 1996, 1♀, (P. Oromí, num. 3191 UB). *Vilaflor*: El Pinalito, 20–27 December 1984, 1♂1♀, (J.M. Peraza, num. 2608 MCNT); 16–23 February 1985, 1♀, (J.M. Peraza, num. 2607 MCNT); 1♂1♀ (J.M. Peraza, num. 2610 MCNT). *Dysdera obscuripes*: **TENERIFE**: *Arico*: Barranco del Rio, in I, 1♂ paratype, (Wunderlich, num. 2626 JW); 27 January 1985, 1♀ paratype, (Wunderlich, num. 2628 JW). *La Laguna*: El Moquinal, 20 April 1990, 1♂ (P. Oromí, num. 2620 SMF). *La Orotava*: Cañadas del Teide, ?, 1♂ paratype, (Wunderlich, num. 2622 JW).

Distribution.—Tenerifean endemic. The most widespread species in Tenerife. It has been collected throughout the island, with the exception of the middle-northern slope.

Comments.—Examination of several paratypes of *D. obscuripes* showed that no diagnostic feature exists when compared with *D. propinqua* holotype. The females used by Simon in the original description of *D. insulana* were also available for study. The author himself (Simon 1907) transferred these females to *D. nesiotis* Simon 1907. The study of the specimens revealed that they were neither *D. insulana* nor *D. nesiotis*, while they perfectly fit those characters of *D. propinqua*. The male type specimens of *D. nesiotis* are the only known specimens of this species so far.

Dysdera unguimmanis Ribera, Ferrández & Blasco 1985

Figs. 173–177, 187–189, Table 15

Dysdera unguimmanis Ribera, Ferrández & Blasco 1985: 57–59, fig. 2A–E [♀]. Holotype female from Cueva del Viento-Sobrado, Icod de los Vinos, Tenerife, Canary Islands; 10 February 1982, J.L. Martín leg.; num. T-CV-121; Stored at UL. Examined. -Wunderlich 1991: 284–286.

Diagnosis.—*Dysdera unguimmanis* is distinguished from all other *Dysdera* species by absence of eyes, remarkable elongation of appendages, reduction of body pigmentation and uniquely large tarsal claws (Fig. 187).

Description.—*Holotype female*: Figs. 173–177. Carapace (Fig. 173) 2.73 mm long; maximum width 2.02 mm; minimum width 1.12 mm. Pale yellow, uniformly distributed; smooth with some small black granular texture mainly at front; hairy, covered with black

Table 15.—Intraspecific spination variability of *Dysdera unguimmani*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	0-1.0.0	0	0	0-1.0.0-1
Tibia 4 dorsal	1.0.1	0	0	1.0.1
Tibia 3 ventral	0	0	0	0-1.0.0
Tibia 4 ventral	0	0	0	0-1.0.0-1

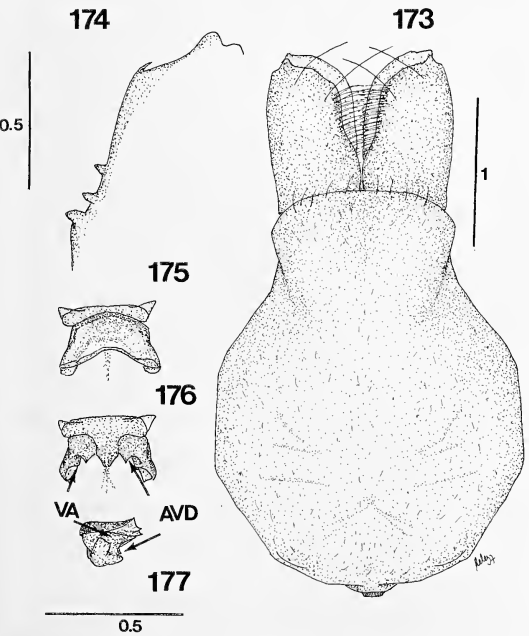
hairs mainly at lateral and back borders. Frontal border roughly round, markedly smaller than ½ carapace length; anterior lateral borders parallel, long; sharpened at maximum dorsal width point, back lateral borders straight; back margin wide, straight. Eyeless. Labium trapezoid-shaped, base wider than distal part; as long as wide at base (square-like); semicircular groove at tip. Sternum yellow, uniformly distributed; smooth; covered in hairs mainly on margin.

Chelicerae (Fig. 174) 1.23 mm long, about ⅓ of carapace length in dorsal view; fang medium-sized, 0.93 mm; basal segment proximal dorsal side scanty covered with piligerous granulations at internal margin. Chelicera inner groove medium-size, about ⅔ cheliceral

length; armed with three teeth and lamina at base; B > D > M (M, D small); D triangular, located roughly at center of groove; B close to basal lamina; M at middle of B and D. Legs whitish. Lengths of female described above: fe1 3.79 mm (all measurements in mm); pa1 1.64; ti1 3.41; me1 3.29; ta1 1.01; total 13.14; fe2 3.84; pa2 1.64; ti2 3.54; me2 3.03; ta2 1.01; total 13.06; fe3 3.29; pa3 1.39; ti3 2.53; me3 3.03; ta3 1.01; total 11.25; fe4 3.92; pa4 1.52; ti4 3.11; me4 3.41; ta4 1.01; total 12.97; relative length: 1 > 2 > 4 > 3; palp: fe 1.14; pa 0.76; ti 0.88; ta 1.31; total 4.09. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands: proximal 1.0.0; distal 1.0.1; ti3 ventral 2 terminal spines. Fe4 dorsal spineless; ti4 dorsal spines arranged in two bands; proximal 1.0.1; distal 1.0.1; ti4 ventral 2 terminal spines. Dorsal side of frontal legs smooth; ventral side of palp smooth. Claws markedly bent; with 10–14 teeth, in two groups, slender, unusually long (Fig. 187).

Abdomen 6.9 mm long; cream-colored; cylindrical. Abdominal dorsal hairs 0.072–0.09 mm long; thin, curved, compressed, pointed; uniformly, scanty distributed. Vulva (Figs. 175–177) rectangle-like (?); wider than long; DF wide. MF well-developed; sclerotized at frontal part. VA frontal region completely sclerotized; posterior region sclerotized at anterior area; tooth-shaped expansion from back border; not joined to lateral sclerotization, about half of DF lateral margins. AVD clearly recognizable. S attachment projected under VA; arms as long as DA, clearly curved; tips not projected; neck as wide as arms. TB usual shape. ALS (Figs. 188–189) with PS; remaining piriform spigots more external than MS, arranged in one row; 3 + 1 piriform gland spigots. PMS, PLS with fewer than 5 acini-form gland spigots.

Male: Unknown.



Figures 173–177.—*Dysdera unguimmani*. 173, Carapace, dorsal; 174, Left chelicera, ventral; 175, Vulva, dorsal; 176, Vulva, ventral; 177, Vulva, lateral. Scale bars in mm.

Table 16.—Intraspecific spination variability of *Dysdera volcania*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.0.1	0	0	1.0.0
Tibia 4 dorsal	0.0.1	1.0-1.1	0	1.0.1
Tibia 3 ventral	1.1.0	0	0	1.0.0
Tibia 4 ventral	1.1.1	0	0	1.0.1

Intraspecific variation.—DA arch-like in dorsal view. Spination variability in Table 15.

Additional material examined.—**TENERIFE:** *Icod de los Vinos*: Cueva de Felipe Reventón, 17 March 1984, 1juv. (J.J. Hernández, num. 2584 UL); 10 September 1992, 1juv. (P. Oromí, num. 2535 UB); November 1993, 1♀ (Arnedo & Ribera, num. 4829 (T44) UB). *Cueva del Viento-Sobrado*, 10 September 1992, 1juv. (H. Enghoff, num. 2630 ZMK); 19 October 1994, 1juv. (Arnedo & Ribera, num. 4822 (T33) UB); 9 June 1996, 1juv. (P. Oromí, num. 3174 UB). *La Orotava*: Cueva del Buncio, 30 October 1991, 1juv. (P. Oromí, num. 2540 UL).

Distribution.—Tenerifean endemic. Known from several lava tubes located on the northern slope of the island.

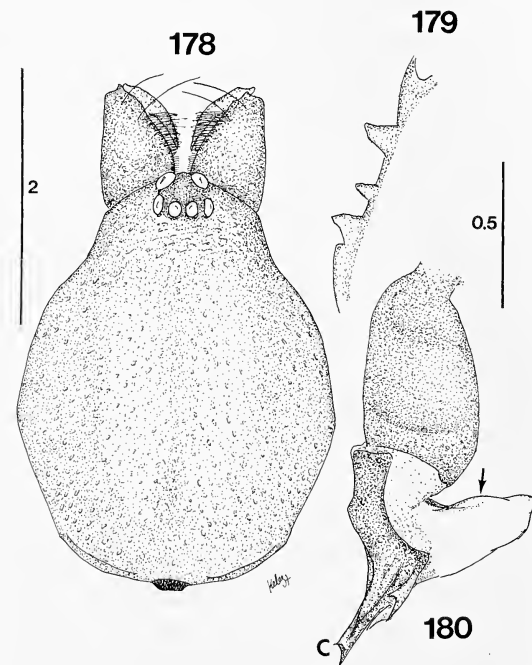
Dysdera volcania Ribera, Ferrández & Blasco 1985
Figs. 178–186, Table 16

Dysdera volcania Ribera, Ferrández & Blasco 1985: 59–61, fig. 3A–D [♂] (♂; non ♀, incorrect identification). Holotype male from Cueva de Felipe Reventón, Icod de los Vinos, Tenerife, Canary Islands; 10 February 1982, P. Oromí leg.; num. T-FR-106; Stored at UL. Examined. -Wunderlich 1991: 284–287.

Diagnosis.—*Dysdera volcania* is distinguished from other Canarian *Dysdera*, except *D. montanetensis* and *D. gibbifera*, by male bulb having distinctly expanded and unsclerotized upper margin of posterior apophysis (P) (Fig. 179). It differs from *D. montanetensis* and *D. gibbifera* by its markedly foveate carapace.

Description.—*Holotype male*: Figs. 178–186. Carapace (Fig. 178) 3.5 mm long; maximum width 2.5 mm; minimum width 1.44 mm. Dark red, darkened at borders; heavily wrinkled, foveate, covered with tiny granulations. Frontal border roughly round, markedly smaller than ½ carapace length; anterior lateral borders divergent; rounded at maximum dorsal width point, back lateral borders rounded; back margin wide, straight. AME diameter 0.24 mm; PLE 0.21 mm; PME 0.15 mm; AME on edge of frontal border, separated one from another about ½ of diameter, close to PLE; PME about ¼ of diameter apart, about ⅓ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base (rectangle-like); semi-circular groove at tip. Sternum dark red, uniformly distributed; wrinkled; covered in hairs mainly on margin.

Chelicerae (Fig. 179) 1.30 mm long, about ⅓ of carapace length in dorsal view; fang short, 0.88 mm; basal segment dorsal, ventral side completely covered with large piligerous granulations. Chelicera inner groove short, about ⅓ cheliceral length; armed with three



Figures 178–180.—*Dysdera volcania*. 178, Carapace, dorsal; 179, Left chelicera, ventral; 180, Left male bulb, external. Scale bars in mm.

teeth and lamina at base; D = Bmt M (or D slightly larger; D,B large); D trapezoid, located near segment tip; B close to basal lamina; M close to B. Legs orange. Lengths of male described above: fe1 3.36 mm (all measurements in mm); pa1 1.99; ti1 2.78; me1 2.78; ta1 0.76; total 11.67; fe2 3.16; pa2 1.89; ti2 2.65; me2 2.78; ta2 0.76; total 11.24; fe3 2.65; pa3 1.26; ti3 1.89; me3 2.6; ta3 0.68; total 9.08; fe4 3.67; pa4 1.64; ti4 2.86; me4 3.59; ta4 0.83; total 12.59; relative length: $4 > 1 > 2 > 3$; palp: fe 1.77; pa 0.93; ti 1.01; ta 1.06; total 4.77. Spination: palp, leg1, leg2 spineless. Fe3 dorsal spineless; ti3 dorsal spines arranged in two bands; proximal 1.0.1; distal 1.0.0; ti3 ventral spines arranged in two bands: proximal 1.1.0; distal 1.0.0; with two terminal spines. Fe4 dorsal spineless; ti4 dorsal spines arranged in three bands: proximal 0.0.0-1; medial-proximal 1.1.1; distal 1.0.1; ti4 ventral spines arranged in two bands: proximal 1.1.1; distal 1.0.1; with two terminal spines. Dorsal side of front legs covered with a piligerous, fine-textured, granular surface; ventral side of palp scarcely covered with a piligerous, fine-textured granular surface. Claws with more than 20 teeth, slender, length twice claw width.

Abdomen 4 mm long; whitish; cylindrical. Abdominal dorsal hairs 0.063 mm long; medium thickness, roughly straight, not compressed, blunt, tip not enlarged; uniformly, scantily distributed.

Male bulb: (Fig. 180) T as long as DD; external, internal distal border sloped backwards. DD slightly bent in lateral view, roughly 45°; internal distal border not expanded. ES more sclerotized than IS; IS continuous to tip. DD tip (Figs. 181–183) straight in lateral view. C present, short; distal end on DD internal tip; poorly developed; located far from DD distal tip; proximal border continuously decreasing; distal border sloping in its base, upper tip projected, pointed; external side smooth. AC absent. LF present; distally not projected; poorly developed. L well-developed; external border not sclerotized, laterally markedly folded; distal border divergent, continuous. AL present, hardly visible except for a small notch; proximal border in posterior view fused with DH. P (Fig. 184) fused to T; markedly sloped on its proximal part, perpendicular on distal; lateral length markedly longer than T width; ridge present, not sclero-

tized, perpendicular to T, distinctly expanded, rounded; upper margin smooth; not distally projected; back margin not folded.

ALS (Figs. 185–186) with PS; remaining piriform spigots more external than MS, arranged in two rows; 6 + 1 piriform gland spigots; PMS, PLS with 10–15 aciniform gland spigots.

Female: Unknown.

Intraspecific variation.—Male cephalothorax ranges in length from 3.35–3.50 mm. AME separation from $\frac{1}{2}$ – $\frac{3}{5}$ of diameter. PLE-PME from $\frac{1}{5}$ – $\frac{2}{5}$ diameter apart. D markedly larger than B. Spination variability in Table 16.

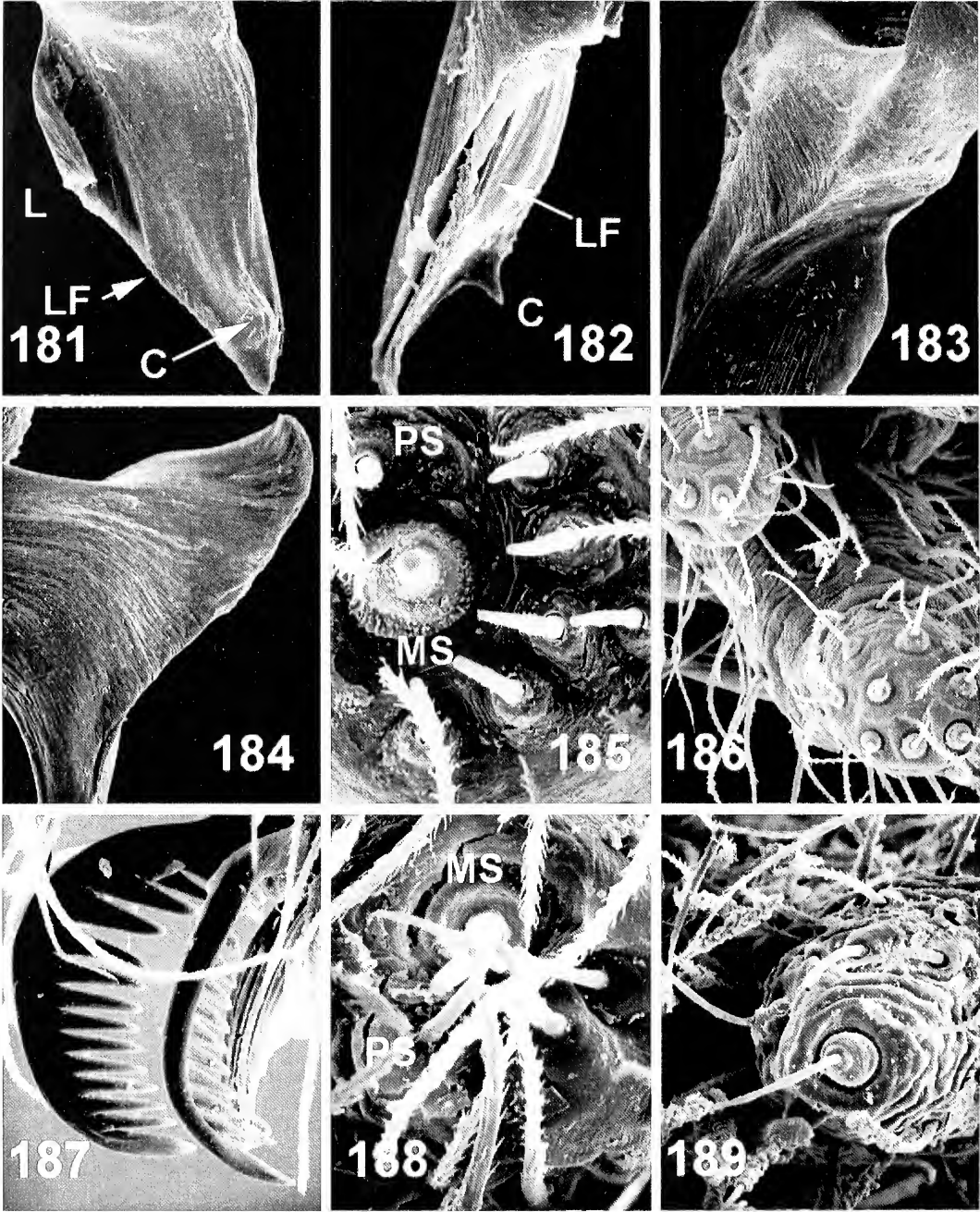
Additional material examined.—**TENERIFE:** *Icod de los Vinos*: Cueva de Felipe Reventón, 12 April 1986, 1♂ (A.L. Medina, num. 2714 UL).

Distribution.—Tenerifean endemic. Known from a single locality, a lava tube located on middle-northern slope of the island.

Comments.—Examination of the allotype female specimen used in the original description of *D. volcania*, revealed that it actually corresponded to a *D. cribellata* female specimen. Schmidt (1975) reported the presence of *Dysdera rugichelis* Simon 1907 in Tenerife, based on the study of a single male specimen. No other specimen belonging to this species has been documented afterwards, although this is a very abundant and widespread species in La Gomera and La Palma (Arnedo et al. 1996). This record is considered to be doubtful, probably due to incorrect identification. This suggestion is further supported by the proved misidentification of another *D. rugichelis* specimen described by the same author as a new species (Schmidt 1981).

DISCUSSION

Even though a lot of new material has been available for the present study, several species remain poorly known. In 8 out of the 22 species discussed, one of the sexes is still unknown (*D. chioensis*, *D. curvisetae*, *D. gibbifera*, *D. gollumi*, *D. hernandezii*, *D. labradaensi*, *D. unguimmanis* and *D. volcania*). In addition, some species have been recorded only once, or are known from a single locality. On the other hand, although several expeditions have been conducted with the main goal of collecting *Dysdera* specimens throughout the island, several island regions



Figures 181–189.—181–186, *Dysdera volcania*, right male bulb and spinnerets. 181, DD frontal; 182, DD external; 183, DD posterior; 184, P internal; 185, Right ALS; 186, Right PMS (upper), PLS (lower). 187–189, *Dysdera unguimmanis*. 187 leg I claws; 188 Right ALS; 189, Right PMS (upper), PLS (lower).

remain undersampled or poorly known. In spite of incompleteness, present data permit limited discussion of ecological and distributional patterns.

As has been reported for other Canarian is-

lands (Arnedo et al. 1996; Arnedo & Ribera 1997), the level of insular endemism is extremely high: 18 out of the 21 species documented in Tenerife, roughly 85% of the species, are endemics. Three species are shared

with neighbor islands: two are found in Gran Canaria (*D. iguanensis* and *D. insulana*) and a third (*D. levipes*) is found in both La Gomera and Gran Canaria.

Distributional patterns are the result of both ecological factors and geological history. Humidity may be considered as the major ecological factor governing *Dysdera* distribution. Most of the species have been documented to occur on the northern slope of the islands from 400–1200 m, which is the most humid region of the island. This humid belt can be further extended to include localities on south-eastern-western slopes where the summit barely reaches 1200 m. Some locations, in spite of being on the dry southern slopes, are actually humid because they are close to nearly permanent watercourses (Barranco del Río) or correspond to the MSS (Barranco del Chorrillo station). Nevertheless, there are some exceptions to the rule, and some species have been reported to live in genuinely dry areas. The taxa *D. macra* and *D. propinqua* have widespread distributions that include humid northern locations as well as very dry places at the high-elevation environments from Las Cañadas or at the southwestern slopes. The only species that has been documented exclusively from dry regions is *D. guayota*. Further investigation of possible physiological adaptations of this species should be conducted in the future.

The geological history of Tenerife is very complex, mainly because of the several volcanic processes involved in its formation. Vulcanism in the Canaries, unlike other oceanic archipelagos (e.g., Hawaiian Islands), is a recurrent process. Several studies, using K-Ar dating, have supplied a large number of data on the age determination of Tenerife (Ancochea et al. 1990 and references herein). They provide a well-documented picture of the volcanic evolution of the island. As recently as 2 Mya, Tenerife was split into three different islands that roughly corresponded to the present-day Anaga, Teno and Roque Conde massifs (Fig. 3). These primitive islands originated in the late Miocene and after several volcanic pulses, volcanic activity ceased about 3.5–4.5 Mya ago. Lava flows from a new volcanic cycle, about 1.9 Mya ago, connected the three massifs and formed Las Cañadas caldera. Volcanic activity in this area has been more or less continuous until historical

ages. Finally, between 0.83 and 0.78 Mya the large ‘valleys’ of Güímar and La Orotava were formed, probably due to a massive landslide. Anaga, Teno and Roque massifs have been considered by several authors as refugial areas or sources of colonizers (Machado 1976; Cobolli Sbordoni et al. 1991; Oromí et al. 1991; Avanzati et al. 1994; Juan et al. 1996). This hypothesis is mainly based on (a) their original isolation (b) the absence of eruptions during the last 4,000,000 years and (c) an extensive surface transformation and habitat destruction in the rest of the island, from 2 Mya ago until the present. There are many examples of distributions from a wide array of taxa that apparently suit this suggested scenario. Tenerifean *Dysdera* provide additional cases which could fit the former hypothesis. Some species have been found exclusively in one of the massifs: *D. insulana* is known only from Anaga and closer localities, while *D. gibbifera* has been collected only in Teno massif and proximities. However, the remaining species have wider distributions. Whether these distributions are the result of dispersal events from some of the mentioned massifs remains to be tested, especially by means of a phylogeographic framework.

Sympatry is another outstanding feature of Canarian *Dysdera* species in general, and Tenerifean ones in particular. As many as four species have been collected in the same locality. In our experience, it was not strange to find two specimens from different species under the same stone. More surprisingly, with a single exception (Cueva del Chío), all the lava tubes where troglobitic *Dysdera* species have been reported hold more than one species. Obviously, such a pattern can only be the result of strong ecological segregation. No close association between any *Dysdera* species and a particular plant community has been observed. In general, species distribution range over two or more different ecological zones. In addition, some species have been collected in areas where original forest has been disturbed by reforestation or introduction of alien plant species. The genus *Dysdera* has frequently been described as a specialist predator of woodlice (Cooke 1965), although a recent study on *D. crocota* prey-preference (Pollard et al. 1995) has shown that this species is better considered as a generalist predator. Whatever taxonomic prey-preference exists in *Dys-*

dera species, it is clear that this is strongly constrained from a morphological point of view by body and chelicera-fang size. Tenerife harbors both the largest (*D. labradaensis*) and the smallest (*D. minutissima*) *Dysdera* species ever reported. In addition, there is a wide spectrum of chelicera-fang sizes and, in a lesser degree, of shapes. Experimental studies regarding prey-preference segregation will constitute a promising field of investigation.

Troglobitic species deserve further consideration. Seven Tenerifean species have been collected exclusively in lava tubes and show morphological evidence of adaptation to the hypogean environment. The cave-dwelling *D. ratonensis* from La Palma is the single case of troglomorphy in the Canaries outside Tenerife. Some of the 'a priori' troglomorphic characters held by these species include: eye reduction or loss, appendage elongation and depigmentation. However, these characters are unequally manifested by the different species. For instance, *D. labradaensis* and *D. chioensis* have eyes markedly reduced in size, all of them being present, while *D. unguimmanis* is completely eyeless. In general, the degree of troglomorphy in Canarian species may be considered low, and in most cases it is restricted to eye reduction (Wunderlich 1993). In contrast, *D. unguimmanis* is one of the most troglomorphic taxa in the genus described to date. Apart from the absence of eyes, the noticeable leg elongation and nearly complete depigmentation, this species has an unusual development of the leg claws (unguis). This feature has been observed only in dysderid cave-dwelling species of the genera *Stalita* Schiödte 1847 and *Folkia* Kratochví 1970 and has been considered as a troglomorphic adaptation in collembolans (Christiansen 1961) and cixiid planthoppers (Howarth 1991).

Even though hypogean *Dysdera* in Tenerife have been found exclusively in lava tubes, several observations suggest that more probably *Dysdera* troglobites originated in, or are at least able to disperse through, the so-called mesocavernous shallow stratum (MSS) (Oromí et al. 1986). This hypothesis is supported by the fact that (a) lava tubes have a geologically short time-span (between 0.3–0.5 Mya), (b) two or more hypogean species usually coexist in the same lava tube and (c) they have relatively wide distributional ranges, as shown by the distance between some of the lava tubes where they have been collected.

Finally, considerations regarding morphological affinities as well as inferences about speciation and adaptations to particular environments, i.e., troglomorphy, are avoided in this paper, since they are better discussed in the light of a cladogram for the species.

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ANTERIOR MEDIAN EYES OF *LYCOSA TARENTULA* (ARANEAE, LYCOSIDAE) DETECT POLARIZED LIGHT: BEHAVIORAL EXPERIMENTS AND ELECTRORETINOGRAPHIC ANALYSIS

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ABSTRACT. We studied solar light cues that may be used by *Lycosa tarentula* (Linnaeus 1758) (Araneae, Lycosidae) for homing. Experiments performed under clear skies, under overcast skies, and under clear skies as seen through a plastic sheet (which changed the polarization from linear to elliptical), allowed us to discover which attributes of daylight were used by the spiders during orientation and homing. We found that patterns of linearly polarized light in the natural sky were sufficient to allow accurate homing by the spiders. The homing behavior of individuals having the anterior median eyes (AME) or all other eyes blinded allowed us to determine that AME were responsible for the reception of polarized light. Electroretinography of all eyes confirmed that only the anterior median eyes were differentially sensitive to the orientation of polarization in linearly polarized light.

Arthropods are known to detect linearly polarized light by means of structural specializations of their eyes, whether compound or single ocellar. An orthogonal arrangement of rhabdoms in certain parts of the retina is the anatomical basis of polarized light perception (for review see Wehner 1989). This has been demonstrated in the compound eyes of some insects. A retinal specialization, called “POL area” (Wehner & Strasser 1985), is located in the marginal dorsal part of the compound eyes and oriented towards the zenith when the animal is walking. In other insects, for example in the water bug *Notonecta glauca*, the POL area occurs in the ventral rather than dorsal part of the eye; and this insect uses polarized light reflected from the water surface to detect the ponds into which it dives (Schwind 1984). It has been experimentally shown that the polarization-sensitive POL area plays a role in celestial navigation in *Cataglyphis* spp. (Wehner 1982) and *Apis mellifera* (Wehner & Rosset 1985; Wehner & Strasser 1985). These Hymenoptera were unable to orient themselves correctly when the POL area was masked.

For spiders, Wehner (1992) reviews the processes and mechanisms by which they can return home: they can use idiothetic, tactochemical or visual information for homing.

Linearly-polarized light is among the visual cues used by some spiders. In this group, an orthogonal disposition of rhabdoms in the ventral part of the retina of the anterior median eyes (AME) has been found in the agelenid *Agelena gracilens* C.L. Koch 1841 (see Schröer 1976) and the lycosid *Lycosa tarentula* (Linnaeus 1758) (see Kovoort et al. 1993), and in the peripheral part of the retina of *L. erythronatha* Lucas 1836 and *L. thorelli* (Keyserling 1876) (see Melamed & Trujillo-Cenoz 1966), while Baccetti & Bedini (1964) could not find a similar arrangement in the lycosid *Arctosa variana* C.L. Koch 1847. In *A. variana*, Magni et al. (1965) analyzed the electroretinographic responses of the different eyes to polarized light. They found that both AME and PME (posterior median eyes) are capable of analyzing the plane of polarized light.

Behavioral studies on orientation by polarized light in spiders were initiated by Papi (1955a, b) in lycosids and by Görner (1958) in agelenids. Both investigators found that the only eyes involved in polarized-light detection were the AME (Görner & Claas 1985; Magni et al. 1964). Papi & Syrjämäki (1963) studied the orientation of an Arctic population of *Lycosa fluviatilis*(= *Pardosa agricola* (Thorell

1856)), which exhibited a correct solar orientation throughout the day.

In the present study, the ability of *Lycosa tarentula* to use celestial cues, mainly the polarized light pattern of the sky, for homing was examined experimentally. The role of the anterior median eyes in the expression of this behavior was determined through eye-painting experiments, and polarization sensitivity was studied by electroretinography of all the eyes.

METHODS

Subjects.—*Lycosa tarentula* is a ground-living lycosid which constructs a burrow nearly 15 cm in depth and 3 cm in diameter. As do the other members of the family, it has eight eyes arranged in three rows. The front row is composed of the anterior lateral eyes (ALE) and anterior median eyes (AME). The middle row comprises the posterior median eyes (PME); and the posterior one, the posterior lateral eyes (PLE). This spider is active during the day and at night.

Experiments were performed on adult females of *L. tarentula* collected at Canto Blanco, 25 km from Madrid. They were captured as immature individuals and maintained in the laboratory under an artificial light/dark cycle of 12:12 h (light on at 0800 h local time) and at 25 ± 2 °C. They were fed with mealflies (*Calliphora vomitoria*) and crickets (*Acheta domestica*). Spiders were used for experiments at least 5 days after their last molt. Voucher specimens of the adults have been deposited in the Muséum National d'Histoire Naturelle (Paris, France).

Behavioral experiments.—Adult females were transferred from their individual containers to a terrarium measuring $60 \times 30 \times 35$ cm placed on the roof of the Faculty building. This terrarium had a 15 cm deep substratum of soil; in the middle of one long side of the terrarium, an artificial burrow was built, similar to that which the spider digs in the field.

Experimental procedure. After 5 days of habituation to the terrarium, experiments began. Spiders were gently pushed forward in one of two paths running, right or left from the burrow, along half-the-length and the full width of the terrarium (Fig. 1). The orientation of the shortest return path was 30° NE for one direction and 300° NW for the other and a distance of 35 cm. When the spider arrived at the end of the path, it was placed into a trans-

parent open glass container and transferred to the center of an open field 90 cm in diameter, and left in the center of it, and in a different direction from that of the burrow. The walls of the open field were 60 cm high and completely white. The periphery was divided into 10° sectors to identify the direction followed by the spider. The position of the spider was recorded when it was at 40 cm from the center.

Experiments were carried out under five conditions, in all cases with the sun obscured by an opaque screen (Table 1). Eyes were made non-functional by covering them with three coats of black paint (Pelikan Hobby Tempera #11).

It was further ensured that the acrylic plastic (a PlexiglasTM sheet with a polyethylene film) changed linearly-polarized light to elliptically-polarized light with maximum efficiency at a specific angle between the electric field of the light and the orientation of the sheet. This arrangement was accomplished by using a He/Ne laser ($\lambda = 632.8$ nm) and introducing the Plexiglas sheet or the polyethylene film between crossed polarizers, together with a Soleil-Babinet compensator. We were able to compensate for the phase change introduced by the sheet and produce zero light at the detector. The transmission characteristics of this sheet, measured with a spectrophotometer (Hitachi U-2000), are shown in Fig. 2.

Statistical analysis. The directions followed by the animals are shown as circular distributions, which were analyzed using circular statistics (Batschelet 1981), calculating the mean resultant vector for every distribution. Appendix I shows how we calculated the mean angle of the sample and the angular deviation and it describes the Rayleigh and Mardia-Watson-Wheeler tests. The statistical evidence of directness was tested following the Rayleigh test. If directness was evident, the confidence interval for the mean angle was calculated to test whether the mean direction of the sample deviated significantly from the direction of the burrow. For each condition (e.g., overcast sky, blue sky, etc.) the Mardia-Watson-Wheeler test was used to test whether the two samples (animals that should orient towards 30° NE versus animals that should orient towards 300° NW) differed significantly from each other.

Electroretinographic analysis.—*Lycosa*

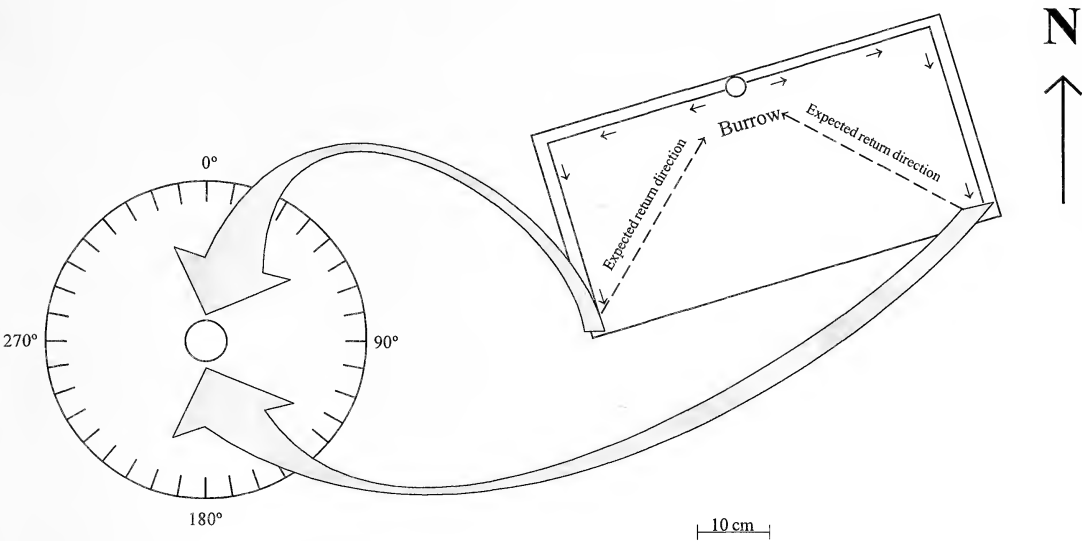


Figure 1.—Apparatus used to study homing in *L. tarentula*. Right, top view of terrarium in which the animal lived during the study; arrows indicate the possible outward paths. Left, dorsal view of the open field in which the animal was left after being taken from one of the corners opposite to the burrow. 0° was always oriented towards the north. The big arrow indicates the translation of the animal to the center of the open field (shown at half of its actual size in relation to the terrarium).

tarentula females from Canto Blanco (Madrid, Spain) were maintained in the laboratory, in Paris, at 20 °C and under natural light-dark cycles (LD: 10/14). Animal weight was about 2 g. Diurnal electroretinograms were obtained as described in Carricaburu et al. (1990). For the recording of ERGs, the animals were placed on a metallic plate used as the indifferent electrode. The different elec-

trode was a thin wire, positioned on the cornea by means of a Prior micromanipulator. The electrodes were connected to a high input impedance solid state amplifier. The animal, the micromanipulator and the amplifier were enclosed in a Faraday cage. The output of the amplifier was connected to a cathode ray oscillator (CRO), the ERGs were displayed on the screen and photographed. The light stimuli

Table 1.—Experimental conditions that were used in this study and cues available to the spiders in each one.

Experimental conditions	Cues available to the spider
Releases under a clear sky	Linearly polarized light pattern
All eyes functional	Light intensity gradient
	Unintended landmarks
Releases under an overcast sky	Unintended landmarks
All eyes functional	
Releases under a clear sky filtered through plastic	Elliptically polarized light pattern
All eyes functional	Light intensity gradient
	Unintended landmarks
Releases under a clear sky	Linearly polarized light pattern
Only anterior median eyes not functional	Light intensity gradient
	Unintended landmarks
Releases under a clear sky	Linearly polarized light pattern
Only anterior median eyes functional	Light intensity gradient
	Unintended landmarks

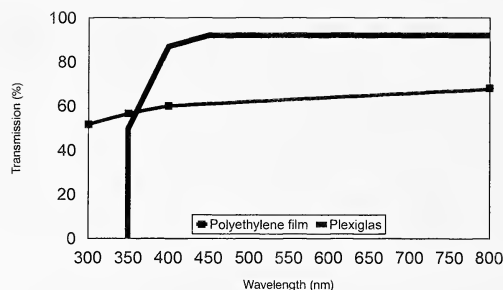


Figure 2.—Transmission (%) characteristics of the components of the plastic sheet.

were given by an electronic flash and were conveyed to the eyes by an optic fiber. A small device was placed between the tip of the fiber and the eyes making it possible to insert one of two polarizing sheets (Polaroid) and consequently to stimulate the eye by linearly polarized light, the plane of polarization being either vertical or horizontal. A light flash was delivered to adapt the eye to light and after a variable lapse of time named duration of dark adaptation, a second flash elicited the recorded ERG. The durations of dark adaptation were 1 s, 2 s, 5 s, 10 s, 20 s, 60 s, and 300 s. In arachnids, the full ERG is composed of two negative waves, β and γ , and a positive wave, δ (Fig. 3), in contrast to insects, in which there is a first positive wave, α , prior to β , γ , and δ (Fouchard & Carricaburu 1972). For each ERG, the amplitude (between the isoelectric line and the top of the β wave) and the latency (between the stimulus and the top of the β wave) were measured: both were found to be highly dependent on dark-adaptation and the hour of recording.

Experiments were carried out on three animals for 24 hours. Only one spider provided a complete electroretinographic record series, without any trouble. Results shown in Fig. 6 relate to this animal.

RESULTS

Behavioral experiments.—Releases under a clear sky: As a control, prior to the release of spiders in the open field, the homing behavior of each individual was observed in the terrarium in order to see if it could return home and was well-adapted to the burrow. Only those spiders well-adapted to the burrow (i.e., those immediately entering it upon contact with the first pair of legs) were used in the open-field experiments. Upon release,

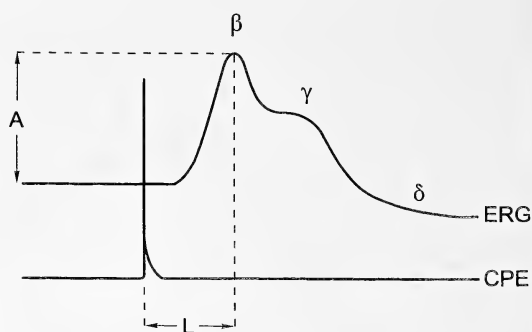


Figure 3.—Electroretinogram of an arachnid. Abbreviations: ERG = electroretinogram; CPE = photoelectric cell response; A = Amplitude; L = Latency.

each spider remained motionless for several minutes and then began to walk following a linear path, sometimes after a turn to re-orient itself. When each spider had run 40 cm or more, it began to make nest-searching movements: legs I and II flexed towards the spider body. These movements have also been observed in the terrarium when the spider was returning to the burrow (the entrance of which had been blocked by soil) and do not occur in other situations. These movements, when seen in the open field, indicated that the spider was in search of its burrow entrance. Figure 4A shows the distribution of movement directions by spiders after open-field releases under a clear sky. The spiders show a correct orientation towards the burrow direction (mean value for 30° NE burrow direction sample: 34° ± 5°, $r = 0.98$, $n = 5$, Rayleigh test: $P < 0.001$; mean value for the 300° NW burrow direction sample: 290° ± 18°, $r = 0.83$, $n = 21$, Rayleigh test: $P < 0.001$), although a bimodal distribution was observed, with some spiders searching for the nest 180° away from it. There was a significant difference between the NE group and the NW group (Mardia-Watson-Wheeler test, $P < 0.01$).

Releases under an overcast sky: Some spiders began by making a systematic search in the open field. This behavior consisted of circular movements by the animals beginning at the release point and increasing in radius with time. From time to time the spider returned to the release point. Such spiders were not included in the analysis. Figure 4B shows that the orientation of the rest of the spiders under an overcast sky was random (mean value for

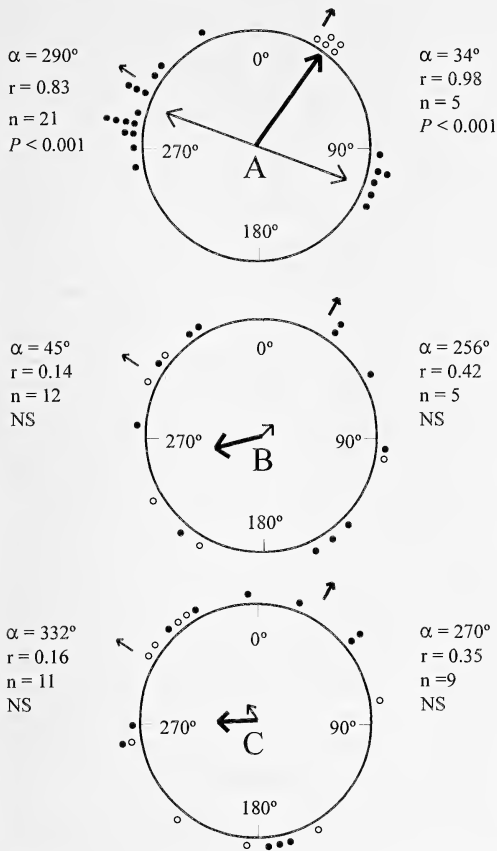


Figure 4.—Directions followed by individual spiders in the open field under different conditions. A = Releases under a clear sky; B = Releases under an overcast sky; C = Releases under the plastic sheet. Arrows outside of the circles point toward the two possible directions for returning to the nest, according to the outbound paths: 30° (thick arrow) and 300° (thin arrow). Filled circles correspond to home directions of animals that should orient to 300°, while open circles correspond to home directions of animals that should orient to 30°. The thick arrow inside the circle is the mean vector direction for the sample of animals that should return to 30°; the thin arrow inside the circle is the mean vector direction for the sample of animals that should return to 300°. Abbreviations: α = mean vector direction; r = length of the mean vector; n = sample size.

30° NE burrow direction sample: 256°, $r = 0.42$, $n = 5$, Rayleigh test: $P = 0.440$; mean value for 300° NW burrow direction sample: 45°, $r = 0.14$, $n = 12$, Rayleigh test: $P = 0.797$). There was no significant difference between the samples (Mardia-Watson-Wheeler test, NS).

Releases under a plastic sheet: As indicated in the Methods section, when sun light passes through the plastic sheet, its polarization changes from linear, which is its predominant characteristic (Waterman 1981), to elliptical, with a small modification of intensity. Spiders released in the open field in these conditions either exhibited the behavior of systematic search or headed in a random direction, as they did under an overcast sky. Only the latter individuals were considered in the analysis. Fig. 4C shows that (mean value for 30° NE burrow direction sample: 270°, $r = 0.35$, $n = 9$, Rayleigh test: $P = 0.342$; mean value for 300° NW burrow direction sample: 332°, $r = 0.16$, $n = 11$, Rayleigh test: $P = 0.710$). There was no significant difference between the NE group and the NW group (Mardia-Watson-Wheeler test, $P > 0.368$).

Releases with AMEs blinded: When the AMEs were blinded by black opaque paint, a non-directed distribution was observed (Fig. 5A). In this case, spiders did not show the systematic search behavior described in Experiments B and C. The behavior of these animals was completely normal except that their orientation was not to the burrow (mean value for 30° NE burrow direction sample: 45°, $r = 0.04$, $n = 6$, Rayleigh test: $P > 0.900$; mean value for 300° NW burrow direction sample: 144°, $r = 0.22$, $n = 10$, Rayleigh test: $P = 0.574$). There was no significant difference between the NE group and the NW group samples (Mardia-Watson-Wheeler test, NS).

Releases with PMEs, PLEs, and ALEs blinded: When all eyes, except the AMEs, were blinded (Fig. 5B), a clear orientation of the spiders to the burrow direction was observed (mean value for 30° NE burrow direction sample: 31° \pm 5°, $r = 0.97$, $n = 5$, Rayleigh test: $P < 0.001$; mean value for 300° NW burrow direction sample: 298° \pm 20°, $r = 0.90$, $n = 10$, Rayleigh test: $P < 0.001$). There was a significant difference between the NE group and the NW group (Mardia-Watson-Wheeler test, $P < 0.01$).

Electroretinographic analysis.—The electroretinographic responses of the AMEs were very different, depending on the plane of light polarization. During the photophase, vertical polarization resulted in a much higher ERG amplitude than did a horizontal one (Fig. 6 shows the change of amplitude with dark adaptation). A maximum was reached at 20 s of

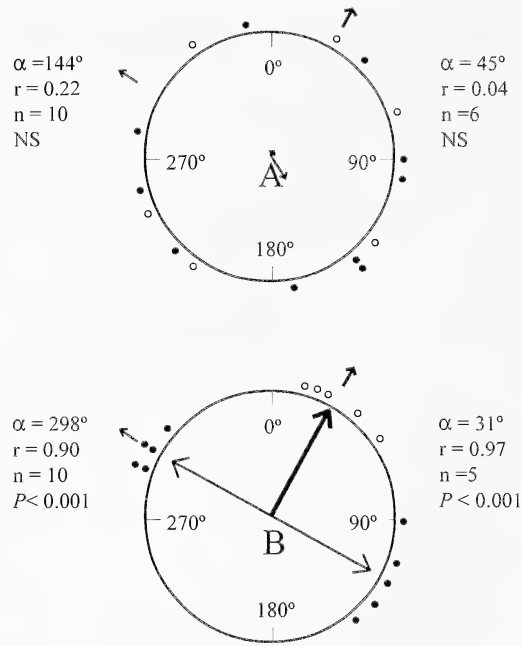


Figure 5.—Directions followed by individual spiders in the open field with different eyes blinded. A = Releases of animals with AMEs blinded. B = Releases of animals with PMEs, PLEs and ALEs blinded. Symbols as in Fig. 4.

dark adaptation, and the amplitude did not change for adaptation up to 5 minutes. Latencies of ERG responses obtained for vertically (5 mn in daytime) or horizontally polarized light were similar, about 30 ms. ERGs of other eyes (ALE, PME and PLE) were not significantly different, whether light was polarized or not.

DISCUSSION

Path integration is a route-based homing which allows the animals a straight return after a more or less winding outward trip (Papi 1992). It is a process that allows an animal to deduce its position, in relation to a point of departure, from its own movement. To achieve this the animal has to measure two components of its outward journey: the direction and the distance. The first component can be measured using external references to calculate the directions followed or using internal references such as centrally stored recordings of their own movements. Following Etienne et al. (1998), "The ability to "home" irrespective of familiar references from the environment remains the hallmark and safest opera-

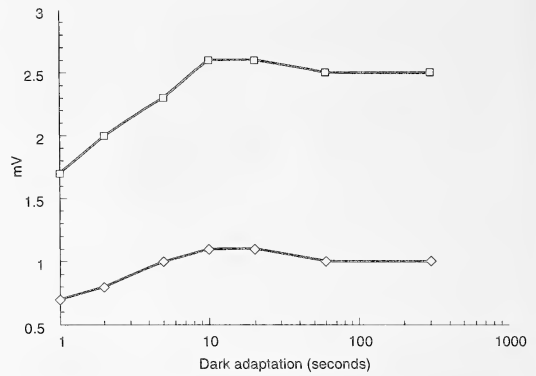


Figure 6.—Electroretinograms (ERG) under polarized light. Diurnal amplitudes (mV) of AME ERGs, recorded for different times of dark adaptation. The \diamond = the horizontal plane of polarization; the \bullet = the vertical plane of polarization.

tional criterion for dead reckoning [path integration]"(p. 56). Our results show that *L. tarentula* is capable of homing by means of a mechanism which does not use familiar references and it is based on visual information as external reference to calculate home direction. In experiments with *Arctosa* (Magni et al. 1964; Papi 1955a, b), the animals were typically placed in the center of a cylinder and their escape directions were registered. They display so-called zonal orientation that generally is not considered as homing (Papi 1992). In contrast, we have used a paradigm that has been used to test homing through path integration in arthropods and mammals (Etienne et al. 1998). In this paradigm, the subjects followed an L-shaped detour and they returned directly to the point of departure. In our study, *L. tarentula* also shows the ability to shortcut the outward path when returning. Generally, our spiders did not retrace the outward path. As with other spiders (Görner & Claas 1985; Seyfarth et al. 1982), *L. tarentula* could use tacto-chemical information, visual, or idiothetic information to return home. Tacto-chemical information is used by lycosid males to find females (reviewed by Tietjen & Rovner 1982), and virgin females of *L. tarentula* leave silk threads placed several millimeters over the substratum (unpubl. data) that can be used by males to recognize females' sexual status and to find them. However, in our study, this information was not available to the animal because the spider was placed in an open field that did not contain

this source of information. Idiothetic information was not used by *L. tarentula* in homing because the spiders did not follow any particular direction under an overcast sky. If *L. tarentula* used idiothetic information, we should have observed successful homing behavior under an overcast sky, as in the idiothetic orientation of blind *Cupiennius salei* (Keyserling 1877) (see Seyfarth et al. 1982) towards a prey from which it has been chased. In this latter ctenid spider it has been argued that homing orientation could be based on non-visual cues, given its nocturnal habits. On the other hand in *L. tarentula*, a diurnal as well as nocturnal spider, visual and non-visual cues can be used for orientation.

Which celestial cues are used by *L. tarentula* to return home? The sun's position is excluded by the experimental conditions of our study. Other cues could be the skylight patterns of linearly-polarized light and the intensity gradient. *L. tarentula* may use these cues since it has a good orientation towards the burrow under a blue sky, while it becomes disoriented under an overcast sky. Under this condition, the spider lacks information about the sun's position and the skylight polarization pattern. We obtained similar results when we used the plastic sheet, which did not significantly modify the intensity gradient but did cancel out the skylight pattern of linearly polarized light. So, we think that the relevant cue for homing is the skylight polarization pattern. In *Arctosa perita* (Latreille 1799) Papi (1955b) also found that this cue was more important for orientation than the light intensity gradient.

How could one explain the presence of a bimodal distribution under a blue sky and with the PMEs, PLEs, and ALEs blinded? We suggest that the time of day at which observations resulting in orientation opposite to the burrow direction were made is the determining factor. These observations were carried out at the first hours of daylight (near sunrise) or when the sun was at its noon location. Under either of these conditions, a symmetrical distribution of the e-vector patterns occurs around the solar-antisolar meridian. So, the spiders tested at these hours could be confused by the symmetry of the e-vector pattern. This would also be the reason for the absence of a bimodal distribution for the animals that should go towards 30° NE under a blue sky and with the

PMEs, PLEs, and ALEs blinded. Although in both samples we are at the low limit of sample size, we think that the results are not invalidated because we have an equal sample size for the animals that should orient towards 30° NE under an overcast sky or with the PMEs, PLEs, and ALEs blinded, and in the latter case the distribution is at random. This bimodal distribution has also been observed in the celestial orientation of sandhoppers (Ugolini et al. 1993) in the morning and at sunset.

The skylight polarization pattern is detected by the anterior median eyes of *L. tarentula*. In *Arctosa variana*, a wandering ripicolous lycosid species, Magni et al. (1964) have shown that polarized light detection is carried out by the AMEs and PMEs. The indirect eyes (PMEs, PLEs and ALEs) have no role in linearly-polarized light detection by *L. tarentula*, since a completely random distribution is observed when the AMEs are blinded. This is in accordance with a morphological analysis of the AME retina (Kovoor et al. 1993) which has shown that, in ventral photoreceptors, successive lines of rhabdoms are oriented orthogonally to each other; such an arrangement was not observed in any other eye type of *L. tarentula*.

From the analysis of the ERGs, it can be concluded that the anterior median eyes of *L. tarentula* perceive polarized light well, which is unlikely for the other eyes. This correlates perfectly with the results of behavioral experiments. The change in the direction of the polarization plane produces a large change in the response (amplitude) of the ERG of the AMEs. During the photophase, *Lycosa tarentula* being inside the burrow in an almost vertical position or outside the burrow with its body axis parallel to the ground, both vertical and horizontal planes of polarization will play a role in homing. Ongoing experiments will determine if a change in the direction of the polarization plane induces a change in the homing direction taken by the spiders as it has been shown for other spiders like *Agelena labyrinthica* (Görner & Claas 1985).

APPENDIX I

Suppose that $\phi_1, \phi_2, \dots, \phi_n$ are the directions taken by n animals to return home, then to calculate the mean angle and the angular deviation of the sample we proceed as follows:

$$\bar{x} = \frac{1}{n}(\cos \Phi_1 + \cos \Phi_2 + \dots + \cos \Phi_n)$$

$$\bar{y} = \frac{1}{n}(\sin \Phi_1 + \sin \Phi_2 + \dots + \sin \Phi_n)$$

and the mean angle of the sample will be

$$\bar{\Phi} = \arctan \frac{\bar{y}}{\bar{x}} \quad \text{if } \bar{x} > 0$$

$$\bar{\Phi} = 180^\circ + \arctan \frac{\bar{y}}{\bar{x}} \quad \text{if } \bar{x} < 0.$$

To calculate the angular deviation we use

$$s = \frac{180^\circ}{\pi} \sqrt{2(1 - r)}.$$

The length of the mean vector, r , is a measure of the dispersion of the data and it is calculated with the following formula

$$r = \frac{1}{n} \left(\sum \cos \Phi_i^2 + \sum \sin \Phi_i^2 \right).$$

With n , sample size, and r , length of mean vector, the Rayleigh test gives us the critical level, P , that the parent population is randomly distributed.

Mardia-Watson-Wheeler test: The purpose of this test is to discover whether two independent samples of n_1 and n_2 observations differ significantly from each other. This test is also known as a uniform-score test because it uses only the order in which the observations of both samples are arranged. We pooled both samples and we ranked the elements of one sample, for example the smallest one. We calculate $\delta = [360^\circ/(n_1 + n_2)]$ where n_1 and n_2 are the sizes of both samples and we multiply each rank by δ , transforming each initial value to β_i . The resultant vector of the first sample has the following components

$$C_1 = \sum \cos \beta_i, \quad S_1 = \sum \sin \beta_i$$

and the length of the resultant vector is $R_1 = \sqrt{C_1^2 + S_1^2}$ and as a test statistic we use $B = R_1^2$.

If $n > 17$, we use the quantity

$$\chi^2 = 2(n-1) \frac{R_1^2}{n_1 n_2}$$

which is approximately distributed as chi-squared with two degrees of freedom.

ACKNOWLEDGMENTS

We wish to thank P. Carricaburu for kindly obtaining the electroretinograms. We also wish to thank J.-M. Cabrera (Fac. Sciences, U.A.M.) for determining the polarization characteristics of the plastic sheet and F. Jaque (Fac. Sciences, U.A.M.) for determining the transmission characteristics of it. We acknowledge J.S. Rovner and an anonymous referee for reviewing the original manuscript and suggesting various changes.

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RESEARCH NOTE

A NEW SPECIES OF THE SPIDER GENUS *ZELOTES* (ARANEAE, GNAPHOSIDAE) FROM CALIFORNIA

Recent sampling near Lake Skinner in southern California has produced the first known specimens of a small species of *Zelotes* that seems most closely related to *Zelotes nanodes* Chamberlin 1936, known only from southeastern Oregon, Nevada, and Utah (Platnick & Shadab 1983). We describe here this new species and provide some notes on its habitat and on other spiders taken in the same samples.

Lake Skinner is surrounded by undisturbed Riversidian coastal sage scrub (Westman 1983) in the Southwestern Riverside County Multispecies Reserve. The new species was collected in June from pitfall traps set in two sampling plots, approximately 600 m and 450 m, respectively, from the lake's northeast shore. The first site (on a north-facing, relatively steep slope), providing one male, has a very dense shrub cover, primarily of *Artemisia californica* Lesson (California sage) and secondarily of *Erigonum fasciculatum* Benthham (California buckwheat) and *Salvia mellifera* E. Greene (black sage) with *Salvia apiana* Jepson (white sage) interspersed among the major shrub components. The composition ratio of the three major shrubs is approximately 4:2:1. The soil consists of decomposed granite of relatively fine particle size mixed with clay; large exposed rocks are absent. The substrate is essentially bare, with sparsely distributed annual *Schismus* grass or, in less exposed areas, a thin lichen cover. Only near the bases of shrubs is any leaf litter present.

The second site (on a south-facing, gentle slope), providing the female and a second male, is vegetated by sparsely distributed shrubs, primarily *E. fasciculatum* and secondarily *A. californicum*, with a few scattered *S. mellifera* shrubs. The composition ratio of the two major shrubs is approximately 2.5:1. The soil here also consists of decomposed granite but has a coarser particle size and a much lower clay content, except in surface depressions

where clay has been deposited by runoff. Between the shrubs, the substrate is bare except for sparsely distributed *Schismus* grass and a few relatively large surface rocks. Leaf litter accumulates only beneath a few of the more closely grouped shrubs. Because of the hard ground surface, few burrows or surface openings of any kind were found; those that were noted opened in surface depressions or in the sandier sections of the plot.

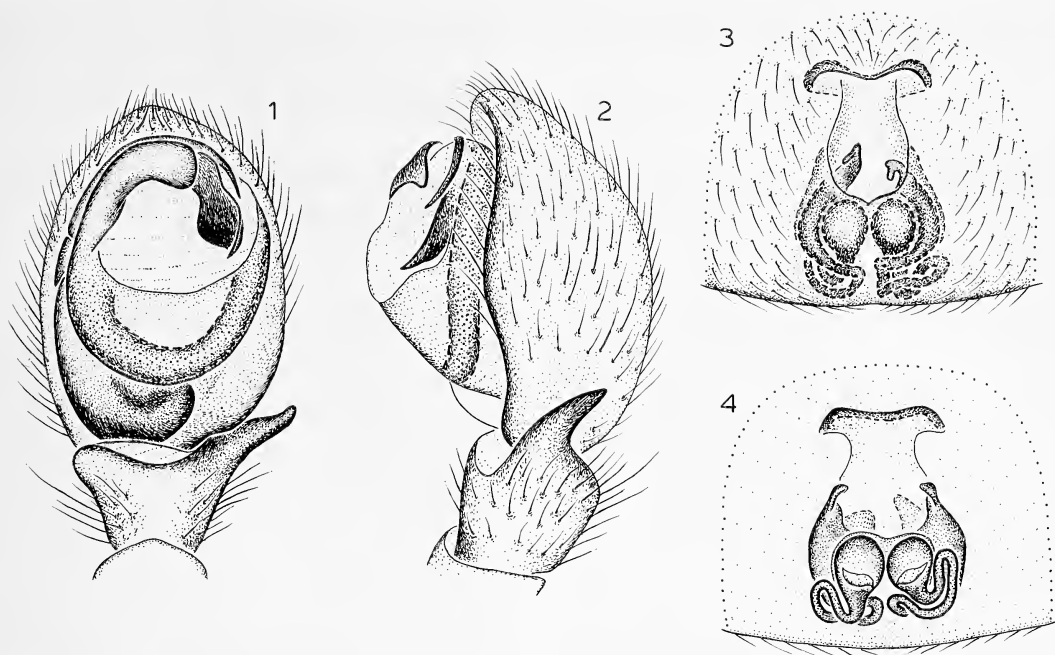
Three other gnaphosid species were collected in the June samples from both plots: *Callilepis gosoga* Chamberlin & Gertsch 1940, *Cesonia classica* Chamberlin 1924, and *Drassyllus insularis* (Banks 1900). The first site also provided *Drassyllus fractus* Chamberlin 1936 and (the probably introduced) *Zelotes nilicola* (O. P.-Cambridge 1874) in June samples, whereas the second site produced *Gnaphosa californica* Banks 1904, *Micaria jeanae* Gertsch 1942, and *Zelotes monachus* Chamberlin 1924. Over 70% of the *Blabomma sanctum* Chamberlin & Ivie 1937 specimens collected (from a possible 24 plots) were taken in December samples from the first site. The second site produced specimens of apparently undescribed species of *Blabomma*, *Aptostichus* (both in December samples), and *Psilochorus* (in June samples).

The format of the description follows that of Platnick & Shadab (1983). We thank Mohammad Shadab of the American Museum of Natural History for help with the illustrations.

Zelotes skinnerensis new species

Figs. 1-4

Types.—Male holotype and female allotype taken in pitfall traps at an elevation of ca. 470 m in a site 450 m from the NE shoreline of Lake Skinner, Southwestern Riverside County Multispecies Reserve, Riverside County, California (♂, 13-16 June, 1998; ♀ 6-10 June 1998, both by T.R. Prentice), de-



Figures 1-4.—*Zelotes skinnerensis* new species. 1, Left male palp, ventral view; 2, Same, retrolateral view; 3, Epigynum, ventral view; 4, Same, dorsal view.

posited in American Museum of Natural History courtesy of Metropolitan Water District of Southern California and R. Redak (Dept. of Entomology, Univ. of California, Riverside).

Etymology.—The specific name refers to the type locality.

Diagnosis.—This species, with its transverse embolus extending across the distal edge of the male palpal bulb, belongs to the *laccus* subgroup of the genus, and is likely to be confused only with what appears to be its sister species, *Z. nannodes*. Males have the distal edge of the terminal apophysis rounded (Fig. 1), whereas in *Z. nannodes* the prolateral edge of the terminal apophysis bears a sharply pointed projection (Platnick & Shadab 1983: figs. 231, 235). Females of the new species have a longer median epigynal plate (Fig. 3) than that found in females of *Z. nannodes* (Platnick & Shadab 1983: fig. 233); the single female available for study has what appear to be fragments of the male embolus extending from the epigynal openings and partially obscuring the median epigynal plate.

Description.—*Male*: Total length 2.49, 2.65. Carapace 1.08, 1.14 long, 0.81, 0.82 wide. Femur II 0.64, 0.66 long. Eye sizes and

interdistances: AME 0.03, ALE 0.05, PME 0.04, PLE 0.05; AME-AME 0.04, AME-ALE 0.01, PME-PME 0.05, PME-PLE 0.00, ALE-PLE 0.05; MOQ length 0.12, front width 0.10, back width 0.12. Embolus shorter than in *Z. nannodes*, without prolateral hump (Figs. 1, 2). Leg spination: tibia IV p1-0-1; metatarsi: III p0-2-2, v2-0-0, r0-1-2; IV p0-2-2.

Female: Total length 3.30. Carapace 1.14 long, 0.88 wide. Femur II 0.67 long. Eye sizes and interdistances: AME 0.03, ALE 0.05, PME 0.05, PLE 0.05; AME-AME 0.04, AME-ALE 0.01, PME-PME 0.04, PME-PLE 0.04, ALE-PLE 0.04; MOQ length 0.11, front width 0.10, back width 0.14. Epigynum with triangular median plate longer than in *Z. nannodes* (Figs. 3, 4). Leg spination: tibiae: III v1r-2-2; IV p1-0-1; metatarsi: I v0-0-0; II v1r-0-0; III p0-2-2, v2-0-0, r0-1-2; IV p0-2-2.

Other material examined.—One male taken in pitfall trap at an elevation of ca. 480 m in a site 600 m from the NE shoreline of Lake Skinner, Southwestern Riverside County Multispecies Reserve, Riverside County, California (6-10 June 1998, T.R. Prentice), deposited in University of California, Riverside.

Distribution.—Known only from the type

locality in Riverside County, southern California.

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RESEARCH NOTE

HARVESTMAN (OPILIONES, GONYLEPTIDAE) TAKES PREY FROM A SPIDER (ARANEAE, CTENIDAE)

The diet of harvestmen has been addressed in several papers which showed that there is large variation in feeding habits (see Gnaspini 1996 for discussion). Several authors considered opilionids in general as predators or possibly as scavengers under natural conditions (Verhoeff 1900; Berland 1949; Bishop 1950; Todd 1950; Whiteley 1961; Juberthie 1964; Cannata 1988; Hillyard & Sankey 1989), as well as in the laboratory (Phillipson 1960; Briggs & Ubick 1981; Adams 1984; Acosta et al. 1995). Some studies done in both laboratory (Bishop 1950; Capocasa & Bruno-Trezza 1964; Edgar 1971; Anuradha & Parthasarathy 1976; Holmberg et al. 1984; Gnaspini 1996) and in nature (Bristowe 1949; Cloudsley-Thomson 1958; Savory 1962) have reported that they accept both animal and plant matter. Therefore, harvestmen seem to be omnivorous, with a preference for animal matter (Gnaspini 1996). Herein we report for the first time a case of a harvestman taking prey from another animal.

The harvestman and spider were observed in nature without touching or altering subjects, and were photographed by the senior author. The observations were made at Reserva Municipal da Mata de Santa Genebra, Campinas, state of São Paulo, Brazil (22°44'S, 47°06'W) on 26 September 1992 at about 2000 h. The temperature was about 25 °C, relative humidity was 60%, and the day was cloudy. Observations were made using a diffuse red light, and pictures were taken using flash. Because of our previous personal observations, we do not believe that the flash photography influenced the behavior of both animals.

The arachnids and prey were not collected. From the photographs, the harvestman was identified as a female *Goniosoma* cf. *longipes* (Roewer 1913) (Gonyleptidae, Goniosomatinae) and the spider as *Enoploctenus cyclothorax* (Bertkau 1880) (Ctenidae). After the proper nomenclatural changes are made, this

is probably the only species of *Enoploctenus* found in Brazil south of Rio de Janeiro (A.D. Brescovit pers. comm.). The moth could not be identified.

The harvestman was first detected on a tree trunk about 20 cm from the spider. The spider was holding the prey (a moth partially wrapped in silk) with its chelicerae (Fig. 1). The harvestman slowly approached the spider, until it touched the spider with its first and second pairs of legs (Fig. 2). The harvestman touched the spider again three or four times. Meanwhile, the spider stood motionless. After 1–2 minutes, the harvestman suddenly moved over the spider, which dropped the prey and backed up about 3–4 cm. Because the harvestman also moved back slightly (ca. 1–2 cm), the prey was now located between the two arachnids (Fig. 3). Just a few seconds later, the harvestman started moving towards the prey, while the spider turned around and moved away (Fig. 4). The harvestman eventually picked the prey up with its pedipalps, and remained at the spot handling the prey (maybe already eating it) for several minutes afterwards.

No cases of prey theft or kleptoparasitism (regularly stealing food from other species) are known for harvestmen in nature. In captivity, several species of North American harvestmen have been observed to tug at and take “prey” (chopped pieces of mealworms) from conspecifics (J.C. Cokendolpher pers. comm.). In the wild, some Brazilian harvestmen have been observed eating prey taken from other animals: members of the genera *Cosmetus* and *Metavononoides* (Cosmetidae) have been observed taking prey from webs of *Blechnoscelis* sp. spiders (Pholcidae) (A.B. Kury pers. comm.); a female *Goniosoma inscriptum* (Mello-Leitão 1922) (Gonyleptidae) was observed eating a homopteran prey wrapped in silk near a *Thwaitesia* sp. spider (Theridiidae) web, in Guapimirim, Rio de Janeiro (R. Pinto-



Figures 1-4.—Sequence of the harvestman *Goniosoma* cf. *longipes* taking a moth from the spider *Enoploctenus cyclothorax*. 1. The spider was holding the prey with its chelicerae when the harvestman was first detected about 20 cm away; 2. Slowly approaching and then touching the spider with its legs; 3. After 1-2 minutes, the harvestman suddenly moved over the spider, and both backed up; 4. Just a few seconds later, the harvestman started moving towards the prey, while the spider turned around and moved away. Scale = ca. 10 mm.

da-Rocha pers. comm.); and a female *Goniosoma longipes* was observed carrying arthropod pieces (dipteran wings and orthopteran legs) wrapped in silk (G. Machado, pers. comm.). These facts may be interpreted either as evidence of prey theft or as the harvestmen having collected abandoned spider prey, perhaps even partially consumed prey. Because kleptoparasitism is defined as a regular procedure of collecting prey from a given species, we do not consider any of these cases to be kleptoparasitism but rather consider them to be opportunistic theft. Kleptoparasitism is a relatively common practice for some species of at least five families of spiders (Coyle et al. 1991). In each of these cases, the kleptoparasitic spiders steal from other species of spiders. In addition, kleptoparasites also are generally much smaller than the host and do not confront the host when stealing the prey.

In order to understand how/why this harvestman succeeded in taking prey from so large a spider, it is important to look at their possible relationships. One of the main predators of goniosomatine harvestmen is the ctenid spider *Ctenus fasciatus* Mello-Leitão 1943, which preys mainly on adult and sub-adult harvestmen (Pinto-da-Rocha 1993; Gnaspini 1996; G. Machado pers. comm.). *Enoploctenus cyclothorax* is common at the entrances of caves where Goniosomatinae harvestmen occur (e.g., *G. spelaum* (Mello-Leitão 1932) from the Ribeira Valley, São Paulo state -Trajano & Gnaspini-Netto 1991; Gnaspini & Trajano 1994), but this spider has never been observed preying on the harvestmen (P.G. pers. obs.). Moreover, during a nocturnal observation (G. Machado, pers. comm.), an adult female *E. cyclothorax* quickly moved over an adult male *G. longipes* which was wandering about near the spider. Immediately after touching the harvestman with its first legs and palps, the spider backed up and stopped, while the harvestman kept on walking in its path, showing no reaction to the spider. The same occurred between *E. cyclothorax* and *G. spelaum* (F.H. Santos pers. comm.). Possibly, the timidity of the species determined their relationships with harvestmen and the possibility of the spider having its prey stolen by a harvestman. *Ctenus* spp. are much more aggressive than *Enoploctenus* spp. (A.D. Brescovit pers. comm.). Other factors involved could be the time since when the

spider last fed as well as the age of the spider (which seemed to be a juvenile, based on size); i.e., juveniles may be less aggressive than adults, although no study on aggressiveness of these spiders has been conducted (A.D. Brescovit pers. comm.). The size of the "thief" may also be important in this kind of behavior—Goniosomatinae are large heavy-bodied harvestmen. Moreover, in the above cited cases observed by Kury and Pinto-da-Rocha, the harvestmen were always bigger (in body dimensions) than the spider, which could have prevented the spiders from protecting themselves from the theft.

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RESEARCH NOTE

ESCAPE BEHAVIOR MEDIATED BY NEGATIVE PHOTOTAXIS IN THE SCORPION *PARUROCTONUS UTAHENSIS* (SCORPIONES, VAEJOVIDAE)

Desert grassland scorpions, *Paruroctonus utahensis* (Williams 1968), are nocturnal, sand-dwelling arachnids that inhabit relatively open, easily accessible sand dune systems. They maintain individual home burrows from which they emerge at night to hunt and to which they return. In general, scorpions can orient in low light levels (Fleissner 1977b) and may be less active during a full moon (Warburg & Polis 1990).

Both positive and negative responses to light have been observed for a large number of arthropods, yet little is known about the effect of light on scorpion behavior. In an early study of vinegaroons (Uropygids), another group of arachnids, tests on photoreceptive behavior provided evidence of a negative phototactic response (Patten 1917, 1919). One of the first studies to examine this behavior in scorpions was by Abushama (1964), who used a simple two-choice behavioral test chamber with illumination directed from the side and found that the scorpion *Leiurus quinquestriatus* Erenberg 1828 (Buthidae) exhibits a negative phototactic response. Subsequent researchers (Jander 1965; Torres & Heatwole 1967; Zwicky 1970b) examined orientation behavior in several arthropods, including scorpions, and observed negative phototaxis. Apart from these studies and the effect of photoreception on circadian activity patterns (Fleissner 1977a, 1977b, 1985, 1986), the influence of light on scorpion behaviors, such as visually guided orientation, has received little attention.

Most scorpions have two sets of eyes, a medial pair and a lateral set, on their dorsal prosoma. The medial eyes are paired structures located on either side of a mid-sagittal plane through the carapace. The lateral eyes are located along the anterolateral margin of the carapace, can number from 0–5 (3 in *P. utah-*

ensis) and usually, but not always, occur in equal numbers on the two sides (Hjelle 1990). Several studies have shown that the medial eyes have greater visual acuity and spatial discrimination, but lower absolute sensitivity, than the lateral eyes (Machan 1967, 1968; Fleissner 1974, 1977b). The average sensitivity of 8.6×10^{-7} candles·m⁻², suggested for the lateral eyes of *Androctonus australis* Linnaeus 1758 (Buthidae), rivals the sensitivity of the moths of the genus *Ephestia* (Fleissner 1977b).

We have observed that when *P. utahensis* are disturbed outside their burrows they often do not immediately return to their burrows, but rather run toward nearby bushes. Given that scorpions orient in extremely low light levels, and that they possess highly sensitive eyes, we consider here whether these animals may be using visual information to guide such escape movements.

In simulated natural habitats in the laboratory, we have been able to elicit escape behavior (a movement to the arena wall within 20 seconds of being dropped into the arena center) in *P. utahensis*. In this study we used a two-choice experimental apparatus, under both infrared and visible light conditions, and found that scorpions use visible light to escape toward dark regions.

The animals used in this study were collected at night in early 1997 from sandy regions south of El Paso, Texas. Voucher specimens (voucher #626) of *P. utahensis* used in this study have been deposited (by EAC) at Texas A & M University, Department of Entomology Insect Collection, College Station, Texas. Animals were measured, weighed, sexed and maintained in 3.8 liter glass jars containing 250 ml of sand collected from the animals' natural habitat. Animals were maintained and experiments conducted in the ani-

mal laboratory facilities at the University of Oklahoma under constant temperature and humidity (22 °C, RH 55–65%). The testing room was photoperiod reversed to allow for more convenient observations and video recording. The light-dark cycle was set as follows: dark 0840–1830 h and light 1830–0840 h. Animals were fed two small live crickets (*Acheta domestica*) per week and misted with water (20 ml/animal) twice a week.

The testing chamber consisted of a round acrylic plastic (Plexiglas[®]) arena approximately 15 cm tall and 76 cm in diameter. The floor of the arena was covered with 800 ml of autoclaved sand (20 minutes at 130 °C). Encircling the arena was a posterboard shield measuring 74 cm tall and 85 cm in diameter; the part of the shield surrounding one half of the arena (the “dark” side) was black and the part surrounding the other half of the arena (the “light” side) was white. The height of the shield was designed to limit the radius of a test animal’s aerial visual field. Test chambers were monitored by a low-light, infrared-sensitive camera (Panasonic CCTV camera, model #WV-BP314) mounted 1.83 m above the arena center. The camera was necessary to score an animal’s choice during infrared light (IR) trials (the animal was not visible to the experimenter) but not necessary in the white light (WL) trials in which just enough light was available for the experimenter to score the trial. The camera was also needed to produce video records for analysis. A television monitor, used to view IR experiments via the low-light camera, was positioned outside the testing room. A voltage meter (Micontra Digital Multimeter 22-185A) and broad-band solar cell (Radio Shack, silicon solar cell 2 × 4 cm, max ratings 0.55 V, 0.3 amp) were used to ensure that WL and IR intensities remained constant and that IR intensity remained at least 10× the WL intensity. The WL (Radio Shack Krypton mini-lamp, model #272-1150, 2.5 V, 0.430 amp) and IR (Ultrac IR-50FL, 50 W) light sources were centered above the arena at a height of 1.83 m and gave off an illumination level of 0.25 lux (measured using a Pasco scientific photometer, model 9152, calibrated to a 2700 °K tungsten filament lamp). Black felt was hung over the top of the apparatus to reduce overhead visual cues.

To test the effect of visible light on the es-

cape behavior of *P. utahensis*, 20 animals were randomly assigned to one of two groups, A and B (5♂ and 5♀ in each group). Group A was exposed to white light (WL) first and infrared light (IR) second and group B was exposed to IR first and WL second. To eliminate bias in the direction of placement, animals were dropped into the arena center by means of a cylindrical tube (13 cm long and 5 cm in diameter). If an animal did not move within approximately one minute it was removed from the arena and re-dropped. Animals were scored based on their first contact with the arena wall: ‘1’ for contact with the dark side, ‘0’ for contact with the light side. Once a movement was observed and scored, the scorpion was removed from the arena and returned to its jar and the substrate on the arena floor was mixed to eliminate chemical cues that could be used by subsequent animals. Halfway through each light regime (after 25 drops) the sand substrate was removed and fresh substrate was spread on the arena floor. Before each drop, the arena and shield were rotated 45° independently (arena counter-clockwise, shield clockwise) so that no animal encountered the same arena/shield orientation twice. Each animal was tested five non-consecutive times per light regime (approximately 20–30 minutes between each drop) and given at least three days off between the two light treatments. This set of tests was conducted over a two-week period in January 1998 between the times of 0900–1700 h CST.

In order to have video records of movements, the above experiment was repeated under the same conditions except that IR was added to the WL. Groups were reduced to $n = 5$ (3♀, 2♂) due to the limited number of healthy animals available from the first experimental group. These tests were conducted over a two-week period in February–March of 1998, and daily video recording times were as in the first experiment.

For both experiments, the behavioral scores of animals, based on their five drops, were summed and averaged. Scores for each treatment group were compared to a theoretical random score of 2.5 (no light-dark preference) using Wilcoxon’s Signed Rank Test.

To verify that animals were responding to the light conditions of our experiment and not to other sensory cues, such as geomagnetic information or chemical trails, the video re-

cords of the second experiment were reviewed and the animals' initial wall contacts were plotted in three ways: relative to the shield, relative to the arena and relative to the room. These contacts were transcribed to transparencies and then to computer-generated plots for analyses. We calculated the mean vectors (Batschelet 1981) for each animal ($n = 5$, five trials) and the average vector for the test group ($n = 10$, 10 animals). Vectors were calculated in this manner to permit consideration of the data as independent measures. The Rayleigh test for randomness was used to determine the statistical significance of the mean vector for each group (Batschelet 1981).

There was considerable variability in the behavior of animals in our experiments. Some animals moved quickly under both WL and IR light treatments, reaching the arena wall within 5 sec, while others took several minutes to reach the wall. The distance traveled was also variable; some scorpions took a direct route to the dark or light side while others had a more circuitous route. Only 15% of the animals needed to be re-dropped before they initiated escape behavior.

In experiment 1, twenty animals were scored as they made initial contact with the arena wall. The order in which animals were exposed to light (i.e., IR or WL first) did not affect scorpion behavior, and the results for the two groups of animals were therefore combined. The averaged scores for animals in each light treatment group were compared to a hypothetical random score of 2.5. Under WL, animals showed a significant preference for the dark region of the arena ($\bar{x} = 4.18 \pm 0.28$ SE, $P < 0.01$), whereas under IR, the animals did not exhibit a preference ($\bar{x} = 2.65 \pm 0.42$ SE).

The second experiment utilized WL + IR as the visible light source and IR served as the non-visible light source. The scores from this experiment were processed as in the first; again, there was a statistically significant preference for the dark side under WL + IR ($\bar{x} = 3.70 \pm 0.21$ SE, $P < 0.01$) but not IR alone ($\bar{x} = 2.10 \pm 0.43$ SE).

In the second experiment we recorded scorpion movements under both light treatments using the low-light, IR-sensitive camera. Using the video records we noted the animals' initial wall contacts and plotted these in three different ways: relative to fixed

points on the black and white shield, to fixed points in the arena, and to fixed points in the room. When plotted relative to a fixed point on the shield, the data reveal a distinct preference toward the dark side under WL + IR ($P < 0.05$) but not under IR. In contrast, the initial wall contacts did not show any apparent distribution relative to fixed points in the arena or room (Fig. 1).

Our study presents strong evidence that *P. utahensis* can use light to orient. When provided with a choice between black and white sides of an arena, animals demonstrated a significant preference to move toward the dark region under WL but showed no significant preference for either region under IR.

Researchers have previously established negative phototaxis (Angermann 1957; Abushama 1964; Jander 1965; Torres & Heatwole 1967) for several species of scorpion. Scorpions are also known to have chemosensory organs which might contribute to orientation (Abushama 1964; Foelix & Schabronath 1983; Gaffin & Brownell 1992, 1997). We evaluated other cues that were potentially available for orientation by plotting initial wall contacts relative to fixed points in the arena and room. In both cases, initial wall contacts were not significantly grouped along the arena wall, suggesting that neither chemical cues from previous trials nor geomagnetic forces played a role in the scorpion's orientation behavior in our study.

The photoreceptors responsible for mediating the orientation responses we have observed are unknown, but possible candidates include the medial and lateral eyes and metasomatic (tail) photoreceptors. Previous researchers (Zwicky 1970b; Geethabali & Rao 1973) have shown that scorpions with their eyes masked could still orient to darkened regions of test chambers, thus suggesting that the tail photoreceptors are sufficient to guide this behavior.

We found no indication of negative phototaxis under IR illumination which is in line with physiological responses recorded by previous researchers who examined spectral sensitivity in various species of scorpion (Machan 1968; Geethabali & Rao 1973; Fleissner 1985; Zwicky 1968, 1970a). The medial and lateral eyes have been shown to have a peak response in the blue-green (450–500 nm) region of the spectrum, with the lateral eyes

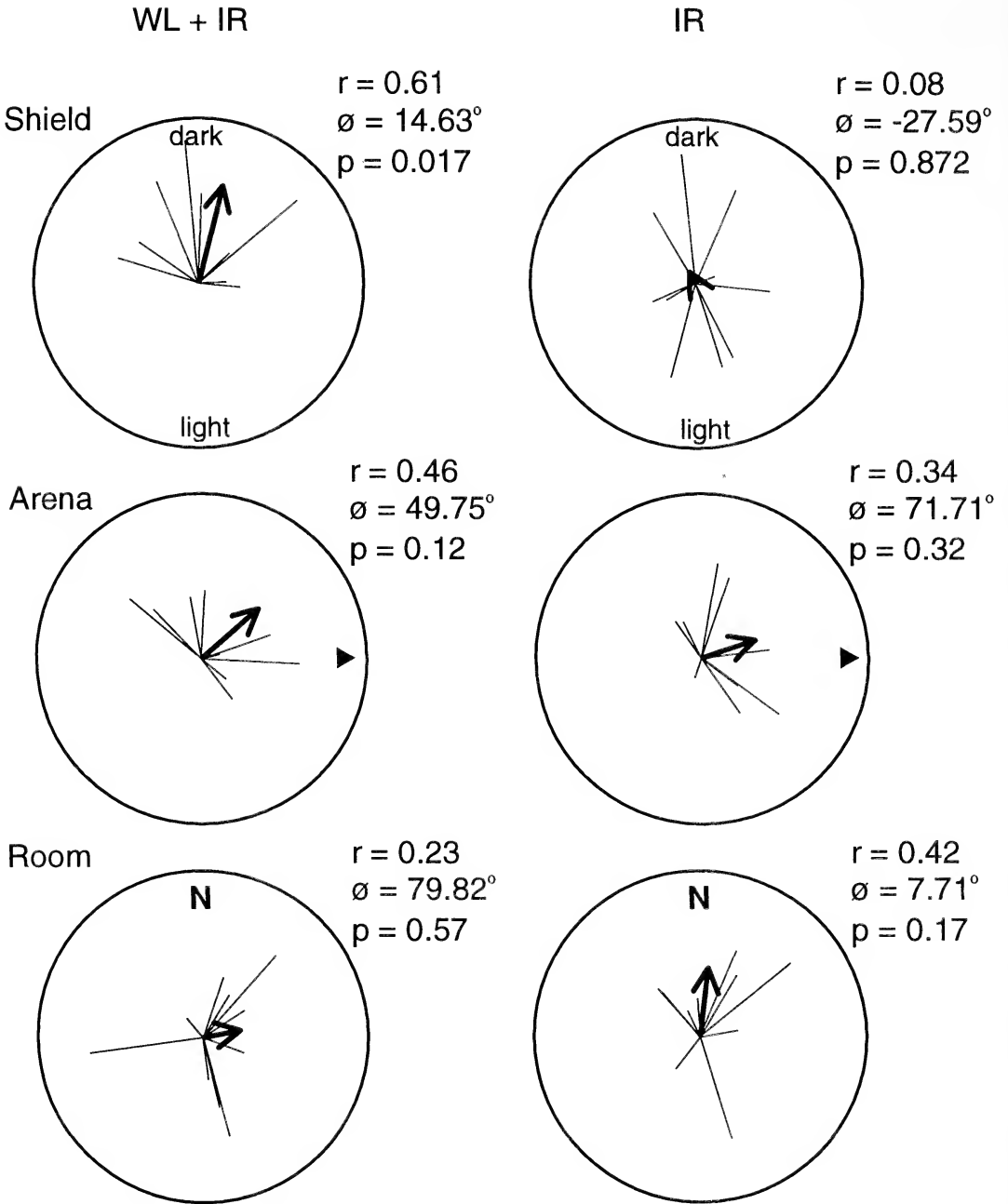


Figure 1.—Scorpion orientation behavior under white light plus infrared light (WL + IR) and infrared light (IR). Animals' initial wall contacts have been plotted relative to the shield, the arena and the room. In each plot, the thin lines indicate the mean vector for each animal, while the thick arrow indicates the mean vector for each group. The light and dark halves of the shield, the arbitrary reference point within the arena (►) and the northerly direction (N) in the room are noted. *Abbreviations:* r = mean length of vector, ϕ = mean angle of vector and P = probability based on Rayleigh tests for randomness.

showing an additional peak in the long ultraviolet (300+ nm) region (Machan 1968). The metasomatic photoreceptors also show sensitivity in the same spectral range (300–500 nm) (Geethabali & Rao 1973; Zwicky 1970b). Furthermore, it is interesting to note that scorpion cuticle fluoresces green under ultraviolet illumination peaking around 450–500 nm (Fasel et al. 1997). Taken together, it is tempting to offer the hypothesis that scorpion cuticle is acting as a light amplifier and that animal movements in our experiments may have been directed by the neural integration of light intensity across the animal's entire cuticular surface.

In this study we have presented evidence of a distinctive, naturalistic behavior that could be used as an assay to resolve some long-standing questions concerning scorpion vision. In particular, this assay could be used to determine which types of photoreceptors are required for orientation and the light intensity threshold necessary for the occurrence of this behavior.

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RESEARCH NOTE

NOTES ON *CYCLOSA INSULANA* (ARANEAE, ARANEIDAE) OF PAPUA NEW GUINEA

The orb weaver *Cyclosa insulana* (Costa 1834) is one of several species within the families Uloboridae and Araneidae that builds stabilimenta, conspicuous silk structures within the orb. Structures referred to as stabilimenta vary considerably among species, and their functions have been hotly debated. Stabilimenta may serve to attract prey (Craig & Bernard 1990) or camouflage the spider against predators (Edmunds 1986; Nentwig & Rogg 1988; Craig & Bernard 1990; Eberhard 1990; Schoener & Spiller 1992; Kerr 1993; Blackledge 1998b) or startle predators (Schoener & Spiller 1992) (see also Nentwig & Ross (1988) who consider neither prey attraction nor camouflage as important). Stabilimenta may also prevent aerial insects and birds from damaging the web by advertizing the presence of the web (Ewer 1972; Horton 1980; Eisner & Nowicki 1983; Kerr 1993; Blackledge 1998a). Phylogenetic data suggest that stabilimenta have evolved several times (Scharff & Coddington 1997), perhaps serving different functions.

Cyclosa (Menge 1866) species exhibit both circular and linear stabilimenta (Edmunds 1986). Camouflaging (Marson 1947; Edmunds 1986; Neet 1990) and stabilizing (Neet 1990) functions have been suggested for the stabilimenta of some *Cyclosa* species, and Tso (1998) found support for the insect-attraction hypothesis in *Cyclosa conica* (Pallas 1772). Here we describe the characteristics of the linear stabilimentum in a population of *C. insulana* in Papua New Guinea. We provide detailed measurements of web characteristics and a small manipulative test of the aposematic (i.e., “web advertisement”) function for stabilimenta. We also compare some unique observations of their mating behavior to those of a previous report (Robinson & Robinson 1980).

Cyclosa insulana ranges from the Mediterranean to Australia. We carried out our field work in Cimbura Province, Papua New Guinea

between 20–31 August 1995. Our field site was located at the Wara Sera Research Station, 10 miles northeast of the village of Haia and approximately 2286 m above sea level. We found *C. insulana* under the eaves of two buildings in areas measuring approximately $3 \times 20 \times 15$ m and $2 \times 6 \times 6$ m. We characterized *C. insulana* webs by measuring (1) web diameter from the two widest points (from the top of the orb to bottom), (2) stabilimentum length and by counting (3) the number of radii and sticky spirals of the webs of 39 adult females and juveniles. Adult males were seen only during courtship on the web of a single adult female. The radii and sticky spirals were numerous and tightly woven, so we counted them twice independently and averaged our findings for each web. Webs that were damaged to a point where we could not accurately assess diameter, number of radii and rings or stabilimentum length were not used in our analyses for that character.

Web and stabilimentum.—A summary of web characteristics is found in Table 1. *Cyclosa insulana* from Spain (Neet 1990) and Burma (Marson 1947) produce both linear and circular stabilimenta. In exposed (windy) sites, spiders produced significantly smaller webs with a greater number of circular stabilimenta than in unexposed (calm) sites (Neet 1990). In our study population, *C. insulana* constructed permanent linear stabilimenta, but no circular stabilimenta; and webs were relatively large (Table 1). Our study site was very well protected from wind, so the most parsimonious explanation is that local conditions have inhibited construction of circular stabilimenta.

The linear stabilimentum of *C. insulana* extends through the hub at its midpoint. Like several spiders of the family Uloboridae (Lubin 1986), *C. insulana* place egg sacs and debris, including plant material, exuviae and prey exoskeletons, in the stabilimenta (Table 2). When sitting at the hub, and at the midpoint of the

Table 1.—Web characteristics. Diameter and stabilimentum length (in cm, mean ± SD) are compared to measurements of *Cyclosa insulana* webs in Balearics, Spain (Neet 1990).

Web characteristics	This study	Neet (1990)	
		Windy (n = 22)	Calm (n = 20)
Diameter	17.9 ± 5.1 (n = 37)	14.4 ± 4.47	11.7 ± 3.44
Radii	51 ± 13 (n = 35)		
Rings	53 ± 10 (n = 31)		
Damage (%)	14.7 ± 16.0		
Linear stabilimentum length	9.1 ± 31.6 (n = 39)	2.25 ± 1.87	2.25 ± 1.29

stabilimentum, the spider folds its legs against its body. This makes the spider appear (to our eyes) virtually indistinguishable from the stabilimentum. It seems likely that the stabilimentum in this species serves to conceal the spider from aerial predators (Neet 1990) and perhaps potential prey. Our measurements show spiders to have dramatically longer stabilimenta than previously reported (Neet 1990). Linear stabilimenta are permanent structures, independent of web renewal (Table 1; pers. obs.). So, under consistently calm conditions, where there would be no advantage in switching to circular stabilimenta, linear stabilimenta are expected to grow longer as prey items and exuviae are added over time.

Stabilimenta may serve to advertize the web

Table 2.—Contents of stabilimenta (n = 10) expressed in terms of the mean number of items found per stabilimentum and the mean proportion of stabilimentum length taken up by items found. Fungi and plant material were estimated only in terms of the proportion of stabilimentum length with fungi and/or plant material.

	Mean number ± SD	Mean proportion of length ± SD
Egg sacs	2.3 ± 2.2	0.24 ± 0.23
Exuviae	2.1 ± 2.0	0.1 ± 0.2
Fungi and/or plant material	n/a	0.1 ± 2.1
Arthropod exoskeletons	4.0 ± 3.0	0.6 ± 0.2
Araneae	0.02 ± 0.63	n/a
Homoptera	0.50 ± 0.85	n/a
Coleoptera	3.0 ± 2.4	n/a
Hemiptera	0.20 ± 0.63	n/a
Diptera	0.20 ± 0.42	n/a
Hymenoptera	0.80 ± 1.14	n/a

to birds and large insects (Ewer 1972; Horton 1980; Eisner & Nowicki 1983; Kerr 1993), which might otherwise damage the web. In our study site, there was an abundance of vespid wasps capable of such damage. Stabilimenta that provided a visual contrast with background structures would be particularly effective as a conspicuous warning signal. Webs at our site were oriented perpendicularly to the ground and in between the wooden posts supporting the buildings, thereby possessing vertical or horizontal backgrounds (specific background for a given web could not be assigned since it is dependent on the direction of approach). We assessed stabilimentum orientation (n = 39) using a circular grid held behind the web, and leveled so that the spider was aligned with the grid origin. The grid was comprised of 16 sections, each 15°, and we recorded the sections through which the stabilimentum passed. Some spiders built slightly nonlinear stabilimenta, but all tended toward a horizontal or vertical orientation (Fig. 1). This tendency might be related to the consistent vertical/horizontal background at this site. A comparison with *C. insulana* webs characterized by more variable backgrounds would provide a test of this possibility.

On the second day of our study, we noted that 2 of the 39 spiders in our study site changed the orientation of their stabilimenta from vertical to horizontal. We hypothesized that stabilimentum orientation was plastic, and that spiders would switch its orientation if the web incurred sufficient damage on the previous day. To test this hypothesis, we chose 20 webs (10 vertical and 10 horizontal stabilimenta) and damaged them by cutting 1 or 2 guylines so that webs collapsed to approximately 2/3 their original size. Examination of the webs on the following day revealed that

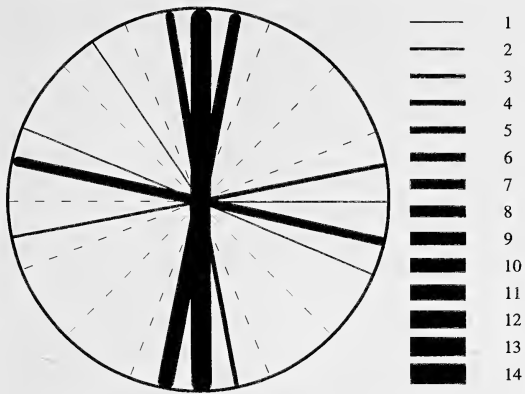


Figure 1.—Stabilimentum orientation. Dashed lines indicate zones on the grid where stabilimenta were marked. Line thickness indicates the relative number of stabilimenta with a particular orientation. Note that several stabilimenta were not perfectly linear, but all tended toward a vertical or horizontal orientation on the web.

none of the stabilimenta orientations had changed, though one was left unrepaired and two spiders had abandoned their location. Thus, it seems that *C. insulana* does not alter stabilimentum orientation in response to web damage. We have no evidence to support the hypothesis that web orientation is manipulated to enhance the conspicuousness of the web against background vegetation. It is possible, however, that the amount of web damage inflicted in our study was not sufficient to evoke this kind of response. A more detailed study involving more extensive and/or different kinds of damage (e.g., to the radii rather than guylines) may provide a better test.

Courtship behavior.—Robinson & Robinson (1980) noted that up to 5 males may congregate on guylines of female's webs where they may court females, rest, or fight and chase other males. The sequence of behaviors exhibited by courting males typically involves (1) the attachment of a mating thread (2) plucking, bobbing, bouncing and high-intensity jerking on the mating thread, (3) and repeated approaches to the female. Female behavior may include (1) no response, (2) approaching the male, (3) plucking the web while facing the male and chasing the male. Contact between the male and female may lead to copulation or rejection of the male by the female (Robinson & Robinson 1980; pers. obs.). Our observations of courtship behav-

iors, though brief, reveal a male-male competition strategy not previously reported in *C. insulana*.

On 25 August 1995, we observed courtship between 0945–1115 h, although courtship took place before and after our observations. Four males lined the periphery of a single female's web, each on separate guylines. Each male advanced along the guyline, apparently laying down silk. As males approached the hub, they plucked the silk vigorously. In response to plucking, the female oriented to the courting male. If the male continued courting, the female advanced toward him. Sometimes the male was chased off the web before contact. If contact occurred, the female struck at the male, the two grappled, and eventually the male fell off the guyline. Males grappled with the female between 1–10 seconds before falling off the guyline. The entire courtship sequence (plucking, approaching, retreating, grappling, striking, and falling) occurred repeatedly. Once, the female seemed to assume a copulatory position for approximately 5 seconds while the male attempted copulation. Before any palpal insertion was observed, however, the female struck the male with her legs, knocking him off the guyline.

Males occasionally plucked the web simultaneously. On two separate occasions, we noted a male traveling around the web frame to the location of another male. After waiting for the other male to begin plucking, he cut a line of silk, effectively eliminating any direct vibratory transmissions between the courting male and the female. It is possible that cutting the guyline also reduced vibratory transmission to other parts of the web (i.e., to the location of other males around the web). After cutting his competitor's guyline, the male returned to his original position on another guyline, and resumed courting. Throughout the day, damage of this kind reduced web size to approximately 40% of its original size. Silk-cutting behaviors have not been previously reported in *C. insulana*. Rovner (1968) noted severe reduction of the female web by courting females of *Linyphia triangularis* (Clerk). However, it is uncertain if this activity has the same function as in *C. insulana*. Male *L. triangularis* performed the silk-cutting whether or not competitor males were present. These males may have been reducing the potential for future suitor competition, or this action

may somehow increase the chances that a female *L. triangularis* will mate.

In addition to this silk-cutting, male-male competition involved plucking silk lines leading to the location of their competitor. On one occasion, an intruding (fifth) male was "chased" away when one of the males plucked the guyline on which he tried to enter the web. These observations are consistent with previous observations of male-male interactions (Robinson & Robinson 1980).

It seems that females have the opportunity to detect signals generated from multiple males. Males apparently compete with other males for access to females by reducing the transmission medium between competing males and the female and perhaps by signaling their status to intruding males. It also seems possible that the opportunity for male choice exists; the quality of the female could be signaled by the mass of the stabilimenta (proportional to the number of prey items and egg sacs present).

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RESEARCH NOTE

THE EFFECT OF FEEDING HISTORY ON RETREAT CONSTRUCTION IN THE WOLF SPIDER *HOGNA HELLUO* (ARANEAE, LYCOSIDAE)

A spider's energetic state has been shown to influence a variety of behaviors. Hungry spiders are more likely to cannibalize one another (Rypstra 1983; 1986), modify their web construction (Henschel & Lubin 1997), and/or may relocate more frequently than sated spiders (Turnbull 1964; Riechert & Tracy 1976; Olive 1982; Uetz 1992; Bradley 1993; McNett & Rypstra 1997). In many species, web site and/or microhabitat selection are also influenced by prey availability (reviewed in Wise 1993). Thus, hunger levels and prey availability influence the behavioral decisions made by spiders. However, not all studies report significant effects of hunger (e.g., Provencher & Riechert 1991). In this study, we investigate the effects of energetic state on retreat construction in the wolf spider *Hogna helluo* (Walckenaer 1837)(Araneae, Lycosidae).

Most wolf spiders are considered to be sit and wait predators which periodically change foraging site (Ford 1978; Stratton 1985). Sensory information from prey (Persons & Uetz 1996), as well as the recent consumption of prey, can increase patch residence time (Ford 1978; Wagner & Wise 1997). In two species of burrowing wolf spiders, Miller (1984) found that prey availability directly influenced burrow site selection.

The wolf spider, *H. helluo*, lives on the soil surface of disturbed riparian areas and is common in agricultural fields. Although it is a vagile hunter, females do construct burrows (Dondale & Redner 1990). In a previous study with this species, we found that hunger level influences locomotor activity (Walker et al. 1999). Hungry animals exhibit higher levels of activity than do satiated animals, which suggests that the time elapsed since last feeding may influence the degree of searching behavior exhibited and patch residence time.

Since this species facultatively constructs burrows, we hypothesized that energetic state also influences burrow construction in this species. Since burrow construction is a potentially energetically expensive endeavor (Marshall 1995), we predicted that adult female *H. helluo* maintained with access to high levels of food would be more likely to construct burrows than would spiders maintained at lower prey levels.

To examine this question, 29 adult female *H. helluo* were randomly assigned to two treatments, high-fed ($n = 14$) and low-fed ($n = 15$). Spiders were fed crickets (*Acheta domesticus*) and were provided with water *ad libitum*. To standardize hunger, all spiders were fed to satiation then starved for one week prior to the experiment. To feed spiders to satiation, individuals were given 3–4 crickets per day for several days. Spiders were considered sated when they refused to consume all the available prey items. Following standardization of hunger levels *H. helluo* were placed individually into 1.4 liter round containers containing 7–11 cm of moist peat moss substrate which had been smoothed to make the surface flat. Animals were then fed either one large (mean = 82.5 ± 5.4 mg) or one small (mean 11.1 ± 0.62 mg) cricket once per week. These crickets were approximately 40% or 10 % of the body mass, respectively, of adult *Hogna*. Seven days later, the presence or absence of a burrow was determined by visually inspecting the containers. Burrows were visually conspicuous because of the presence of a large amount of silk and the disturbance of the soil which had been smooth prior to the introduction of the spider.

To verify that the treatments had an effect on hunger, we estimated body condition on a random sample of eight animals per treatment (a body-size free measure of nutritional state

Table 1.—Mean carapace width and abdomen width (mm) for high and low-fed *Hogna*. Carapace width was not significantly different between high and low-fed spiders; however, abdomen width and body condition of starved spiders was significantly less than fed spiders.

Trait	Treatment	Mean (S.E.)	<i>n</i>	Test statistic and <i>P</i> -value for comparing high and low-fed spiders
Carapace width	High-fed	11.54 (0.235)	8	$t = 1.383, df = 14$
	Low-fed	12.00 (0.234)	8	$P = 0.1884$
Abdomen width	High-fed	11.89 (0.252)	8	$t = 3.878, df = 14$
	Low-fed	9.792 (0.481)	8	$P = 0.0017$
Body condition	High-fed	12.127 (0.323)	8	$F_{(1,13)} = 29.65$
	Low-fed	9.559 (0.323)	8	$P < 0.0001$
Number of spiders with burrows	High-fed	12	14	Fishers Exact Test
	Low-fed	6	15	$P = 0.0209$

or fatness, Jakob et al. 1996). Abdomen and carapace width were measured using an ocular micrometer on a Wild dissecting microscope. Since the data were normally distributed, body condition was estimated as the analysis of covariance adjusted mean of abdomen width using carapace width as the covariate. We used Fisher's Exact test to test the hypothesis that high-fed spiders are more likely to burrow than low-fed spiders.

We found no significant difference in carapace width between high and low fed spiders (Table 1). However, high-fed spiders had wider abdomens than low-fed spiders. High-fed spiders also had significantly higher body condition than did low-fed spiders. These differences suggest that high-fed spiders were in a much better nutritional state than were low-fed spiders. Significantly more high-fed spiders (85%) constructed burrows than did low-fed spiders (Table 1).

Hunger level clearly influenced the probability of burrow construction in *Hogna helluo*. Animals in the high-fed group were much more likely to construct burrows than were animals in the low-fed treatment group. Previous studies have demonstrated that hunger influences locomotor activity in this species. Hungry individuals exhibit high levels of locomotor activity relative to sated individuals (Walker et al. 1999). Those data combined with data from this paper suggest that hunger can play an important role in the behavior of this species.

Hunger does not seem to affect the behavior of spiders equally (see discussion in Provencher & Reichert 1991). Several studies have suggested that hunger is not an important fac-

tor influencing spider behavior (Anderson 1974; Greenstone & Bennet 1978; Provencher & Reichert 1991; Walker et al. 1999). In particular, Anderson (1974) found that *Lycosa lenta* Hentz 1844, another species of lycosid, seem to exhibit normal behavior over a 30-day starvation period. Also, we have found that hunger does not affect locomotor behavior in *Pardosa milvina* (Hentz 1844) (Walker et al. 1999). However, we have found that *H. helluo* is sensitive to recent levels of prey consumption both in activity levels (Walker et al. 1999) and in burrow construction (Table 1). Since burrows represent a considerable energetic investment as their construction requires not only the excavation of soil but also the deposition of silk, the fact that well-fed spiders were more likely to construct them is not surprising. Our data make it tempting to predict that prey availability influences patch choice and residence time in this species. However, because our spiders were confined, we do not know whether well-fed *H. helluo* will build burrows wherever they are or if they are capable of connecting high prey capture with a particular site and using that information to decide whether to construct a burrow.

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RESEARCH NOTE

SURVIVAL OF THE HUNTING SPIDER, *HIBANA VELOX* (ARANEAE, ANYPHAENIDAE), RAISED ON DIFFERENT ARTIFICIAL DIETS¹

Spiders occupy an important part of the overall predatory arthropod fauna in different terrestrial ecosystems (Riechert 1974; Riechert & Lockley 1984). They are also known to play an important role in the regulation of pest species in agriculture (Whitcomb et al. 1963; Dondale et al. 1979; Dean et al. 1982; Mansour et al. 1982; Culin & Yeargan 1983; Mansour et al. 1983; Orazé & Grigarick 1989; Riechert & Bishop 1990; Barrion & Litsinger 1995). Baseline information on life history and biology is fundamental for ecological work and is also important to further investigate the potential of spiders as biological control agents. However, life history studies have been done on very few species of spiders. One reason is the lack of reliable rearing methods to determine life histories and other biological data directly from laboratory cultures. Another reason is the lack of appropriate artificial diets. Since spiders are primarily carnivorous, they require behavioral cues from the prey to initiate attack and feeding (Riechert & Luczak 1982). This makes the rearing and maintenance of spiders in the laboratory a very laborious task. Moreover, it appears that most spiders must feed on a variety of insect prey species to obtain the optimum nutrition for survival and reproduction (Greenstone 1979; Uetz et al. 1992). The need to rear different insect prey species makes it especially difficult to culture spiders in the laboratory. Formulation of artificial diets would greatly facilitate laboratory rearing of spiders; however, knowledge of the complete nutritional requirements for spider is necessary. Recently, it was reported that some species of wandering spiders are facultative nectar feeders (Taylor &

Foster 1996). This could explain the success of some previous works (Peck & Whitcomb 1968; Whitcomb 1967) on rearing spiders in the insectary using artificial diets. This finding of nectivorous feeding behavior inspired us to compare the survival of spiders under different artificial diets. For this study the hunting spider *Hibana* (= *Aysha*) *velox* (Becker 1879) (Anyphaenidae) was selected because it was found to be the dominant species in lime (*Citrus aurantifolia* [Christm.] Swingle 1914) orchards in south Dade County, Florida. Also, its spiderlings were observed to feed on the larvae of citrus leafminer, *Phyllocnistis citrella* Stainton 1856. Voucher specimens of *H. velox* and *P. citrella* are deposited at the Division of Plant Industry (DPI), Gainesville, Florida.

To test the effects of the different artificial diets on the survival of *H. velox*, egg sacs were collected in the field and brought into the laboratory and kept until the eggs hatched. The resulting offspring were used for the experiment. Each spiderling was maintained in a separate container as described by Peck & Whitcomb (1968) with some modifications to prevent cannibalism. Instead of glass tubing with both ends open, common laboratory glass vials (15 mm diameter × 60 mm long) were utilized. The open end was plugged with cotton through which a stemmed cotton swab had been inserted. The cotton swab inside the glass vial was saturated with the artificial diet by dipping. Three different artificial diets were included in the experiment: 30% sucrose solution (cane sugar, Publix Supermarket Inc., Lakeland, Florida); milk + yolk mixture (1 cup homogenized milk + 1 fresh chicken egg yolk), and soybean (non-dairy beverage). Water served as the control. Nutritional composition of the milk + yolk and soybean diets

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Table 1.—Nutritional composition of milk + yolk and soybean diets based on the manufacturer's nutritional analysis and given as amount per 100 ml of media.

Nutrient composition (per 100 ml of media)	Milk + yolk	Soybean
Total fat	3.0 g	1.3 g
Saturated fat	1.3 g	0.0 g
Cholesterol	98.0 mg	0.0 mg
Sodium	83.0 mg	39.0 mg
Total carbohydrates	6.1 g	11.0 g
Sugars	5.2 g	6.5 g
Protein	6.1 g	2.6 g
Potassium	0.0	126.0 mg
Vitamin A	350 IU	0.0 IU
Thiamin (B1)	0.0	0.05 mg
Riboflavin	0.0	0.03 mg
Niacin	0.0	0.52 mg
Pantothenic acid	0.0	0.35 mg
Pyridoxine hydrochloride	0.0	0.05 mg
Folate	0.0	0.02 mg
Vitamin C	0.52 mg	0.0
Vitamin D	44 IU	0.0
Biotin	0.0	2.6 µg
Calcium	139.0 mg	26.0 mg
Iron	0.31 mg	0.31 mg
Phosphorus	0.11 g	0.04 g
Magnesium	0.0	17.4 mg
Zinc	0.0	0.26 mg

are provided (Table 1). Twenty spiderlings were included for each artificial diet. Two replications in time were prepared and kept at 27 °C in different rearing chambers, one at 45% relative humidity (RH) and the other at 80% RH. The two RH conditions were chosen based on work by Peck & Whitcomb (1968) and Taylor & Foster (1996).

At 45% RH, all the spiders on all of the diets died in less than 30 days from the start of the experiment. In contrast, Peck & Whitcomb (1968) reported best survival [42 days for *Chiracanthium inclusum* (Hentz 1847) and 90 days for *Gladicosa* (reported as *Lycosa gulosa* (Walckenaer 1837))] when the spiders were kept at 45% RH. There was no significant difference for the age at death of *H. velox* on different diets. The mean age at death of the spiders kept at 45% RH was 13 days (range, 7–18) on soybean diet; 10 days (range, 8–11) on milk + yolk diet; 12 days (range, 7–16) on 30% sucrose solution; and 11 days (range, 7–14) on water. Spiders kept at 80% RH survived longer, especially spiders on soybean and milk + yolk diets. In 30 days, the percent survival of spiders on soybean diet

(82.5%) was significantly higher ($P \leq 0.05$) than on milk + yolk diet (46%). Spiders raised on 30% sucrose solution and water did not survive for the duration of the experiment. The mean age at death of spiders on sucrose solution was 14 days (range, 5–21); whereas for spiders on water, it was 11 days (range, 8–12). On both soybean and milk + yolk diets, the first mortality occurred at 6 days after the start of the experiment. A drastic increase in mortality was observed on milk + yolk diet from day 6 to day 16 after the start of the experiment; the survival endpoint was reached at day 17 (Fig. 1). Mortality was less on soybean diet; the survival endpoint was at day 12 (Fig. 2). The single mortality at day 21 was due to fungal contamination.

Although the percent survival on soybean diet was significantly higher ($P \leq 0.05$) than on milk + yolk diet, development of the spiders seemed to be delayed. This observation was based on percent molting, time of molting, and carapace width of the spiders. Spiders raised on milk + yolk diet underwent two molts 30 days after the start of the experiment (Fig. 1). The earliest molt was 6 days after the

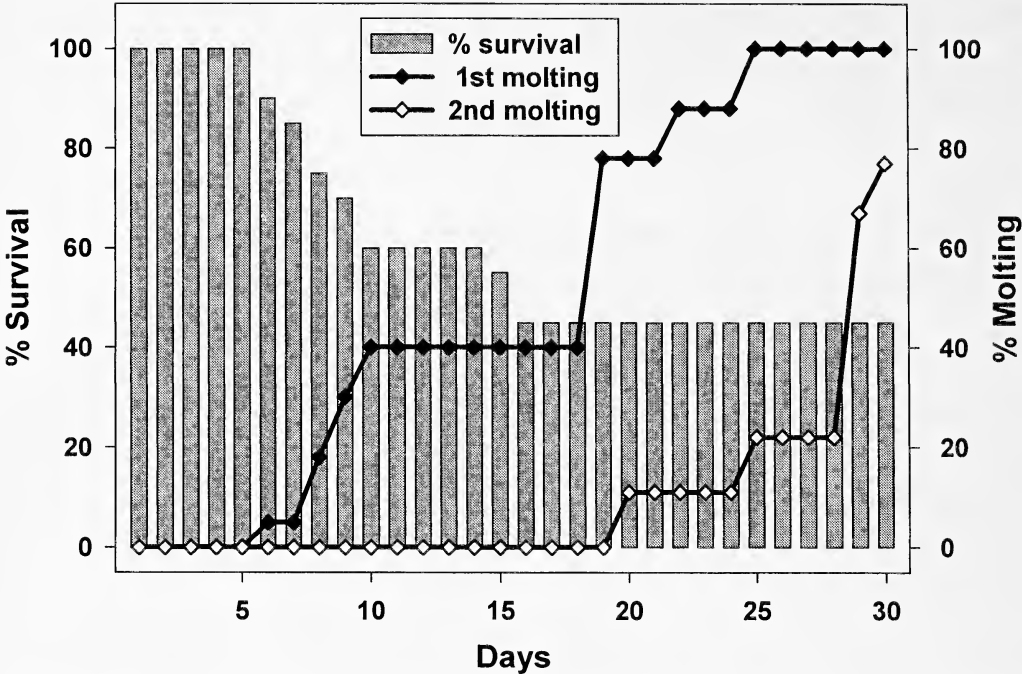


Figure 1.—Percent survival and molting of *Hibana velox* using milk + yolk diet as artificial diet.

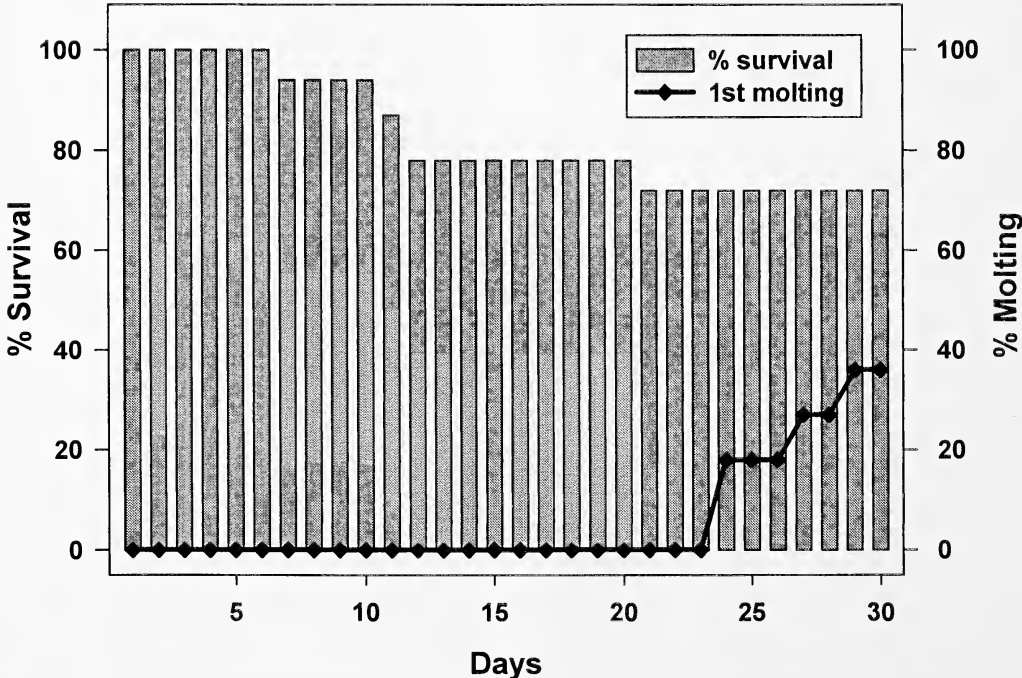


Figure 2.—Percent survival and molting of *Hibana velox* using soybean as artificial diet.

start of the experiment; the mean age at first molt was 17 days (range, 6–30). The mean age at second molt was 25 days (range, 20–30). On soybean diet, the molting of the spiders was late compared to the spiders on milk + yolk diet. The first molt was at 24 days and only 40% of the surviving spiders molted 30 days from the start of the experiment (Fig. 1). The average carapace width of spiders raised on milk + yolk diet was 0.70 mm (range, 0.50–0.85), whereas spiders on soybean diet had an average carapace width of 0.50 mm (range, 0.35–0.58). In general, the carapace width of spiders on milk + yolk diet was more than 25% greater than that of spiders on soybean diet. These findings suggest the importance of supplying more complete nutritional requirements when rearing spiders using artificial diets. The soybean diet is devoid of cholesterol (Table 1) which is the common source of sterol. It was reported that cholesterol is a precursor of ecdysone, the molting hormone (Foelix 1982). This may explain the delayed development of spiders on soybean diet. The milk + yolk diet has a high level of cholesterol, probably contributing to the normal progress of spider development. Nevertheless, the high level of carbohydrates in the soybean diet (Table 1) suggests that carbohydrate could be an important component of the artificial diet for spiders. Carbohydrates are the major energy source important for survival or longevity of any arthropod species (Singh 1984).

In this experiment, we observed that the percent survival of spiders on soybean diet was almost twice that on milk + yolk diet. Furthermore, the drastic increase in mortality of spiders on milk + yolk diet in the first two weeks of rearing the spiders may be avoided if enough carbohydrate is available at that stage of development. From the result of this experiment, we can hypothesize that a combination of soybean and milk + yolk diets could provide more balanced nutritional requirements for wandering spiders. Thus, an experiment to assess the performance of combining soybean and milk + yolk diet on spider survival and development is underway.

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 33, 34, *A-us y-us*, male. Scale = 1.0 mm.

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